Historical Biogeography and Climate Change: application of Ecological niche-based models and GIS to the conservation of African elephants and giraffes

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Sumário

Ecologistas acreditam que a biodiversidade está a atravessar a sexta grande extinção em massa. Enquanto que o clima desempenhou um papel importante em eventos de extinção anteriores, as atividades humanas estão agora a assumir o papel principal. As interacções entre as mudanças climáticas e fragmentação do habitat estão a aumentar as preocupações sobre o futuro da distribuição e abundância das espécies. A fragmentação de habitats está a afectar negativamente espécies já sob pressão, impedindo a movimentação e dispersão. Estima-se que as alterações climáticas forcem as espécies a mudar a sua distribuição, fisiologia e comportamento sazonal. Tentativas para abordar algumas destas questões têm recaído nos modelos de nichos ecológicos. Assumindo o conceito de conservação do nicho (persistência dos requisitos do nicho das espécies) esta abordagem combina pontos de presença de espécies com uma série de variáveis ambientais para prever a disponibilidade de habitat. Incertezas e erros relacionados com os procedimentos de modelação, algoritmos e hipóteses foram levantando questões sobre o impacto destes nos resultados de modelação.

A existência de longos registos históricos e de interações com seres humanos tornam o elefante africano e a girafa espécies ideais para abordar questões metodológicas e ecológicas. O principal objetivo desta tese foi o de comparar os efeitos de modelação dos nichos parciais nas previsões de futuras distribuições de espécies. Distribuições históricas e atuais foram usadas para testar quatro abordagens de modelação em relação à sua sensibilidade para as previsões sob as alterações climáticas e para inferir os efeitos das atividades humanas. Os resultados mostraram um excelente desempenho das técnicas de modelação com excepção para a Análise Factorial do Nicho Ecológico e para os Modelos Lineares Generalizados. A evolução do nicho das espécies modeladas mostrou uma diminuição no espaço climático que foi mais evidente nas girafas. Independentemente dos dados utilizados, as previsões sob alterações climáticas revelaram um aumento na área adequada para o elefante. No entanto, as previsões de área adequada para a girafa tiveram diferentes tendências de acordo com os dados utilizados. Previsões a partir de dados históricos sugerem um aumento na distribuição enquanto que projecções feitas utilizando a distribuição actual sugerem um decréscimo em áreas adequadas. Este estudo realça padrões biogeográficos e futuras áreas adequadas sob o efeito das alterações climáticas. Enfatiza os efeitos das atividades humanas na distribuição das espécies e as consequências, limitações e incertezas associadas à modelação de nichos parciais.

Palavras-chave: Nicho ecológico; Modelação de nicho ecológico; Alterações climáticas Caça furtiva; fragmentação de habitats; elefante africano, girafa.

Abstract

Ecologists believe that biodiversity is under the sixth great extinction wave. Whereas climate has had an important role in previous extinction events, human activities are now assuming the front row. The interactions between climate change and habitat fragmentation are enhancing concerns on future species distribution and abundance. Habitat fragmentation is affecting negatively species already under pressure by precluding movements and dispersal. The human-induced climate change is expected to force species to shift their ranges or to modify their physiology and seasonal behavior. Attempts to address some of these issues have relied on ecological niche based models (ENN). With the assumption of niche conservatism (stability of species niches requirements), this approach combines species occurrences with a series of environmental variables to predict habitat suitability across landscapes. Uncertainties and errors related with modeling procedures, algorithms and assumptions have been raising questions about the impact on modeling results.

The existence of long historical records and interactions with humans make the African elephant and giraffe ideal species to address methodological and ecological issues. The main goal of this thesis was to compare the effects of modeling partial niches in predictions of future species distributions. Current and historical distributions were used to test four modeling approaches regarding their sensitivity to climate change predictions, and to infer the effects of human activities. Results revealed great modeling performance with the exception for the Ecological Niche Factor Analysis and the Generalized Linear Models. The niche evolution of modeled species exposed a decreased in the climatic space that was more evident in giraffes. Regardless of the dataset used, predictions under climate change revealed an increase in suitable area for elephants. The giraffe's predicted suitable area evolves differently according to datasets. Projections from historical data suggest an augment in distribution while projections made based on current distribution suggest a decreased in suitable areas. This study enlightens biogeographic patterns and future suitable areas under climate change. It also emphasizes the effects of human activities in species distributions and the consequences, limitations and uncertainties when modeling partial niches.

Keywords: Ecological niche; Ecological niche-based model; Climate change; Poaching; Habitat fragmentation; African elephant; Giraffe.

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1. Introduction

1.1 Biodiversity loss

Biodiversity is experiencing a worldwide crisis resulting from the increasing levels of species extinctions, habitat loss and human-induced climate change (Brooks *et al.* 2006; Botkin *et al.* 2007). In the past few decades, efforts were made to reverse the situation: conservation societies and communities have been growing in all different scales and political targets have been established (Rands *et al.* 2010). Despite this emergent notoriety in conservation awareness, we are still observing a high rate of biodiversity loss. In fact, ecologists believe that Earth's biota is now already experiencing the sixth great extinction. It is assumed that these massive events of biodiversity loss have been a part of Earth's history. Generally there have been five great mass extinctions during the history of life on this planet, mostly because of geological reasons (Wake and Vredenburg, 2008). The oldest mass extinction occurred at 439 Mya and resulted from great fluctuations in sea level. Marine organisms were severely affected and a significant part simple disappeared. Terrestrial vertebrates had not yet evolved. The next great extinction happened at 364 Mya and a large part of marine life got extinct, however the amphibians, the first terrestrial vertebrates, survived this extinct event. Global cooling after bolide impacts may have been the cause. The third global event was by far the worst of the five mass extinctions, when around 95% of all species (marine and terrestrial) were lost. Scientists are still debating causes, but the intense volcanic activity (caused by a bolide impact), which led to a profound climate change, seems to be the strongest candidate. The next great extinction episode occurred by the end of Triassic (199 – 214 Mya), when the opening of the Atlantic Ocean, caused by the spreading of the sea floor, led to a significant global warming. Mostly marine life was affected and terrestrial organisms also experienced much extinction. The most recent extinction event occurred at 65 Mya and led to the disappearance of the emblematic dinosaurs. Causes are still being debated from diverse climate changes to consequences of the impact of a giant asteroid (Wake and Vredenburg, 2008).

As in previous extinction events, climate is thought to have played an important role, but humans may have had compounding effects. Over the past century, Earth's climate has changed, with increasing temperature and fluctuations in precipitation regimes (Araújo and Rahbek, 2006) and consequences on biodiversity have already

been noticed. These climatic changes are affecting physiology, distribution and phenology of some species, forcing them to adapt to new conditions at a very high pace and ultimately to shift their ranges (Thuiller *et al.*, 2005). The steady overall decline of wild species populations' size, range, condition, and connectivity to other populations and/or patches of suitable habitat (Butchart *et al.*, 2010; Rands *et al.*, 2010), are heightened by human-induced climate change, poaching, land-use transformation and exotic species introduction (Traffic 2008; Butchart *et al.*, 2010). If on one hand the human-induced natural habitat fragmentation and poaching are expected to have a more immediate impact on biodiversity (Hof *et al.,* 2010; Lindsey *et al.,* 2013), the effects of climate change are likely to become a long-term concern with unpredictable consequences. These hazards constitute different threats to biological systems, which can also interact, leading to range contractions and species extinctions (Higgins, 2007). There is an increasing concern over the consequences of poaching (illegal hunting) and fragmentation in species' distribution and the effects of the interactions with climate change (Hof *et al.,* 2010).

1.1.1 Poaching and trading

Conservation problems, such poaching and trading are known for their consequences on biodiversity, from limiting the adaptive value of social relationships to alter the structure of genetic variation within populations (Archie and Chiyo, 2012). Historically, hunting had an important role in daily life of primordial humans from leadership to food source. After the agriculture revolution, the need for survival hunting was reduced, however, even in modern times illegal hunting remains an important part of economy or culture of many countries (Bell *et al.*, 2007; Naylor 2005). The concept of wildlife trade is defined by any sale or exchange of wild animal and plant resources by people. A diverse range of products needed or prized by humans that reached an important marketable value such as hide, ivory, skins, medicinal ingredients, timber, fish and other food products, are commercialized for a wide range of purposes (Bell *et al.*, 2007; Naylor, 2005). Although the primary motivational factor for wildlife traders is economic, ranging from small-scale local income generation to major profit-oriented business, wildlife is hunted and traded for many reasons as cultural and traditional beliefs, aesthetical motivations or even status (Lindsey *et al.,* 2013). Most wildlife trade is probably within national borders, but the international market is growing every year, particularly in Asia (Traffic, 2008; Lindsey *et al.,* 2013). World wildlife trade involves hundreds of millions of individual plants and animals of tens of thousands of species,

adding to a list of endangered fauna a long one of threatened flora (Naylor, 2005). However, not all trading is illegal, wild plants and animals from all over the world are caught or harvested from the wild and then sold lawfully for a multitude of purposes (Lindsey *et al.,* 2013). The problem begins with the unsustainable wildlife trade, namely when this activity threats the survival of many species in the wild. The increasing demand for a variety of sea-foods, leather goods, timbers and medicinal ingredients, and the possibility of illegally trade is seen as a valuable opportunity for human populations living in extreme poverty conditions, usually near to wildlife (Naylor, 2004; Traffic, 2008). Illegal trade is driven by high profit margins and, in many cases, the high prices paid for rare species. The major consequences are reflected on vulnerable species, which cannot keep up with human consumption and are pushed further to the edge of extinction (Naylor, 2005). Animals and plants (or their parts) are nowadays trafficked much like illegal drugs and arms (Naylor, 2005) and this uncontrolled rate of poaching led to extinction of species and are threatening many others (Traffic, 2008; Lindsey *et al.,* 2013). These international networks able to lead the world of illegal wildlife trade are commonly linked to traffic of drugs, arms and people and more recently, to terrorist organizations (WWF - worldwildlife.org). By its very nature, the true scale and value of the wildlife trade are unknown, as much of the trade is carried out through informal networks, and not documented or captured in government statistics and/or illegal, and similarly not recorded (Traffic 2008). However, it is estimated that this market moved over USD300 billion in 2005 (Traffic 2008), ranking as the second most powerful parallel economy, only seconds the traffic of drugs (Naylor, 2005). Additionally, corruption, weak judicial systems and light sentences allow criminal networks to keep plundering wildlife, making the illegal wildlife trade a low risk business with high returns (Lindsey *et al.,* 2013).

This overexploitation of species affects the living planet in wider ways, causing imbalance complex systems with unpredictable consequences for nature and human beings. Ecological consequences of illegal hunting include overall wildlife population declines, reductions in biodiversity, local disappearances of many species from both within and outside protected areas and associated loss of ecosystem functionality, and in some cases, complete collapse and disappearance of wildlife populations (Lindsey *et al.,* 2013). The introduction of invasive species by traders and the incidental killing of animals are some of the collateral effects of a giant business (Naylor, 2005). In the past few decades, awareness regarding this hazard has grown raising the attention to some of the most slaughtered species as rhino, elephant and tiger (See Fig.1) (Bell *et*

al., 2007; Naylor, 2005). However, illegal poaching and trading easily undermine efforts made by countries to protect natural resources. Wildlife trade alone is a major threat to some species, but its impact is frequently made worse by habitat loss and other pressures (Naylor, 2004).

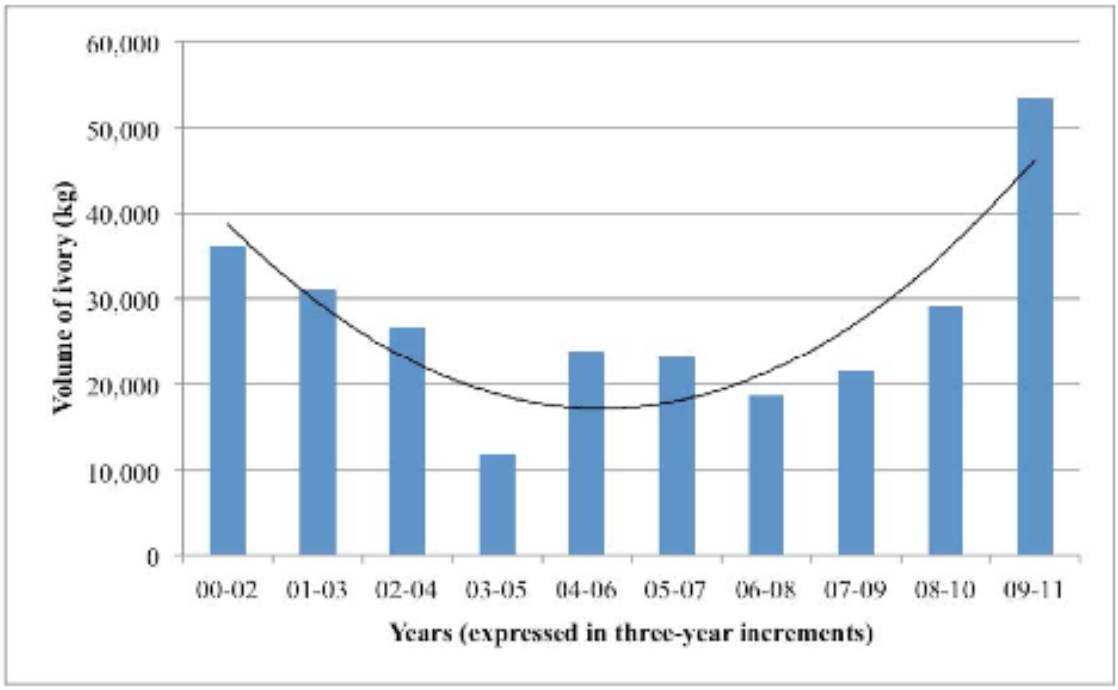

Fig. 1: Large-scale ivory seizure volumes plotted in three-year moving averages by year*, 2000-2011* CITES 2012.

1.1.2 Habitat fragmentation

Habitat fragmentation is widely recognized as one of the main threats to biodiversity (Henle *et al.,* 2004). Species from all taxonomic groups are believed to be affected by its negative effects, especially those with narrow habitat requirements and distributions (Henle *et al.,* 2004). Habitat fragmentation is a landscape-level process in which a continuous habitat is progressively subdivided into multiple, smaller and isolated patches (Fahrig 2003; Fischer and Lindenmayer, 2007). Fragmentation involves changes in landscape composition, structure and functions across scales and result from geological processes, climatic fluctuations and more recently, human activities (McGaridal and Cushman, 2002; Fahrig, 2003). This land transformation can lead to species and population declines (due to limited resources) and isolation increases, affecting negatively day-to-day movements and dispersal (Fischer and Lindenmayer, 2007).

Habitat isolation can negatively affect the behavior of species and their response capacity to others threat factors. The effects of breaking apart a continuous habitat into smaller and isolated patches in populations relapse in low species

richness, low abundance, and increase the risk of population extinction (Battisti, 2003; Bender *et al*., 2003; Fischer and Lindenmayer, 2007). At the species level, isolation can also amplify the pervasive effects of small population size. Smaller habitat patches sustain smaller populations, which show lower genetic and phenotypic variability and increases the vulnerability to demographic fluctuations, inbreeding depression and stochastic events (Battisti, 2003; Bolger *et al.,* 2001; Fahrig, 2003; Fischer and Lindenmayer, 2007; Hof *et al.,* 2011). Beyond affecting species directly, land-use changes have a marked impact on the ability of species to deal with climate change and in turn, climate change enhances the negative impact of habitat and landscape changes (Fischer and Lindenmayer, 2007: Hof *et al*., 2011). The widespread loss and fragmentation of habitats in many areas that would become climatically suitable with future warming are remote from current distributions and beyond the dispersal capacity of many species (Walther *et al.,* 2002).

Habitat connectivity has been hypothesized to increase the persistence of species in fragmented landscapes (Uezu *et al.*, 2005). The rescue effect, migration of individuals between patches, has been suggested as a possible mitigation factor of isolation and fragmentation (Fig. 2). Habitat connectivity is the link between patches of suitable habitat for a given species that could be enhanced through corridors (Fischer and Lindenmayer, 2007). Habitat fragments can be connected through dispersal corridors, which enable the movements of individuals and contribute for connectivity among populations, thus reducing the probability of extinction (Bolger *et al*., 2001). Species with higher dispersal ability, capable of rescue and recolonize distant patches, should have lower extinction risks in highly fragmented habitats (Henle *et al.,* 2004). However, mobile species tend to have larger individual home ranges and the same amount of remaining habitat support fewer individuals. Even with high dispersal power, colonization potential may be considered low because of the individual area requirements. The benefits of dispersal capacity may be counteracted by the smaller population, thus increasing the extinction risk (Henle *et al.,* 2004). Additionally, specialist species are more likely to have discontinuous distributions and hence greater risks of extinction. These species are usually dependent on patchily distributed resources and also have lower probabilities of occurrence in fragments where their niches can be represented (Henle *et al.,* 2004).

Increasing fragmentation of habitat patches is likely to intensify this uneven distribution of the adaptive potential due to the decline of phenotypic and genotypic variability both within and between populations. This reduces the potential of a species

to respond with trait and range shifts, limiting the ability of species to adapt to changing environmental conditions (Hof *et al.,* 2011).

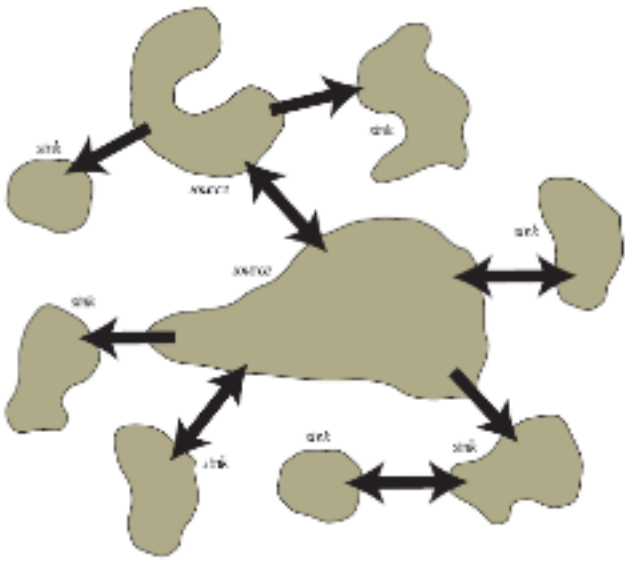

Fig. 2: Hypothetical metapopulation structure in which *sink* populations are rescued by dispersing individuals from *source* populations along suitable habitat connections between population patches.

1.1.3 Climate change

Earth's climate has been changing at an unprecedented rate over the last hundreds of thousands of years, with expected negative impacts for biodiversity (IPCC, 2007; Walther *et al.,* 2002; Araújo and Rahbek, 2006; Hof *et al.,* 2011). The ecological disruption shaped by climate change is generally slower than that caused by other factors but the effects of climate are likely to become increasingly prominent relative to the other factors (Thuiller 2007). Climate warming is likely to affect the phenology, physiology, and distribution of many species and the synergetic combination with other human-induced habitat fragmentation and loss will likely increase range contraction and species extinction (Midgley *et al.,* 2002; Walther *et al.,* 2002; Pimm, 2008). However, organisms, populations and communities do not respond to approximate global averages. Regional changes resulting from the asymmetry of warming are expected to be more relevant in the ecological response to climate change (Walther *et al.,* 2002). The heterogeneous influences of climate change in the ecological dynamics systems raises concerns on how to assess their potential impacts on biodiversity (Walther *et al.,* 2002). Currently, the perception that global warming has affected biodiversity is transversal to a wide range of species from different geographical distributions (Walther *et al.*, 2002; Pimm, 2008). The effects are expected to be

different depending on the ecosystem. Possible consequences in the marine biome will include increased thermal stratification, reduced upwelling of nutrients, decreased pH and loss of sea ice (Thuiller 2007). On the terrestrial side, deserts, grasslands and savannahs in temperate regions are likely to respond to changes in precipitation and warming in various ways. The Mediterranean-type ecosystems will be prompt to develop deserts and grassland and the tropical regions may be affected by altered patterns of natural fires and CO_2. Finally, species living on mountains, particularly sensitive to changed conditions, are expected to migrate upwards but only to a limited extent (Thuiller, 2007). The climatic regimes influence species distributions, often through shifts in species-specific physiological limits of tolerance for temperature and precipitation (Walther *et al.*, 2002; Thuiller, 2007), which are both the key predictors of species' ranges (Pimm, 2008). Although changes in climate will be likely to involve precipitation (Higgins 2007; Thuiller 2007) and temperature shifts, and despite some uncertainty still associated (Sala *et al.*, 2000), the ecological effects of climatic change are varied and multifactor (Walther *et al.*, 2002; Higgins, 2007). Furthermore, the synergistic interactions between drivers of change may decrease in importance whenever biodiversity change responds only to the driver with the greatest impact. Therefore, the consequences of increases in global temperature or complex environmental changes on species distribution are virtually unknown, but forecasts claim that 15–37% of natural species will be "committed to extinction" by 2050 (Sala *et al.,* 2000; Walther *et al.,* 2002; Thuiller, 2007; Pimm, 2008). In the future, the climatic envelope describing the present-day species range may no longer exist, which would affect distribution, abundance, and life cycles of a large number of organisms (Walther *et al.,* 2002; Araújo *et al.,* 2005; Pimm, 2008; Hof *et al.,* 2011). Responses of species to climate change may be synthesized by their ability to "track" shifting climates through colonization of new territories or to modify their physiology and seasonal behaviors (Walther *et al.,* 2002; Thuiller, 2007; Pimm, 2008). Given the unpredictability of climate change effects on biodiversity, some studies are predicting a high extinction rate within some groups and in others no significant changes in future ranges predictions (Araújo and Rahbek, 2006; Jetz, *et al.,* 2007; Pimm, 2008). On the other hand, future spatial distributional may lead to new species interactions by moving apart those that currently interact and approaching those that presently do not coexist (Araújo *et al.,* 2005; Thuiller *et al.,* 2006) Moreover, while some evidences indicated that the ranges of species are shrinking, there are others suggesting that some species may become widespread (Pimm, 2008). With general warming trends, "climate

envelopes" become shifted towards the poles or higher altitudes and species are expected to track the shifting climate (Walther *et al.,* 2002). In fact, species range shifts have already been documented as a response to climate change and in the last century (Araújo and Rahbek, 2006; Thuiller, 2007; Pimm, 2008). However, the synergetic effects between climate change and the ongoing destruction and fragmentation of natural habitats challenges the survival ability of numerous of species (Walther *et al.,* 2002; Jetz *et al.,* 2007; Higgins, 2007; Pimm, 2008; Hof *et al.,* 2011). As a result, species thus far largely unaffected by direct human actions are in danger of extinction from climate change (Pimm, 2008).

The Intergovernmental Panel on Climate Change (IPCC) was established to assess the scientific, technical and socio-economic information relevant for the understanding of human induced climate change. From the five assessments of climate change since 1990, reports have been produced to address the scientific basis of climate change, its impacts, adaptation and mitigation (Le Treut *et al.,* 2007). At the beginning of the 21st century, the IPCC published a set of emission scenarios for use in climate change studies and clustered them in four different narrative storylines (A1, A2, B1, and B2) (Fig. 3). Each storyline describes (regionally and globally) the relationships between forces driving climate change and their predicted evolution during the 21st century according to different demographic, social, economic, technological, and environmental developments that diverge in increasingly irreversible ways. In simple terms, the four scenarios combine two sets of divergent tendencies: one set varying between strong economic values and strong environmental values, while the other set varies between increasing globalization and increasing regionalization. For instance, both A2 and B2 assume regionally oriented economic growth but the population and economic growth are higher in the former. On the contrary, A1 and B1 assume a global oriented growth, but the former takes mainly into account economic growth alone while the latter considers the introduction of clean and resource efficient technologies. Concerning these storylines, six groups of scenarios were then drawn: one group each in the A2, B1 and B2 and three groups in the A1 family, characterizing alternative developments of energy technologies (IPCC-TGICA, 2007). Many studies have predicted future effects of climate change on the distribution of a wide number of species. However, the complexity associated with animal distributions (influenced both by climate, that potentially limits physiological processes, and by vegetation that determines resource availability and also habitat) has biased researches to estimate future distributions in plants and biomes (Midgley *et al.,* 2002; Araújo *et al*., 2005;

Thuiller *et al.*, 2006). In spite of these, distribution models have shown to be highly informative in biogeographic studies and some of the most promising applications of these models are related to poorly known regions where biogeographical data are scarce (Pearson *et al.,* 2007).

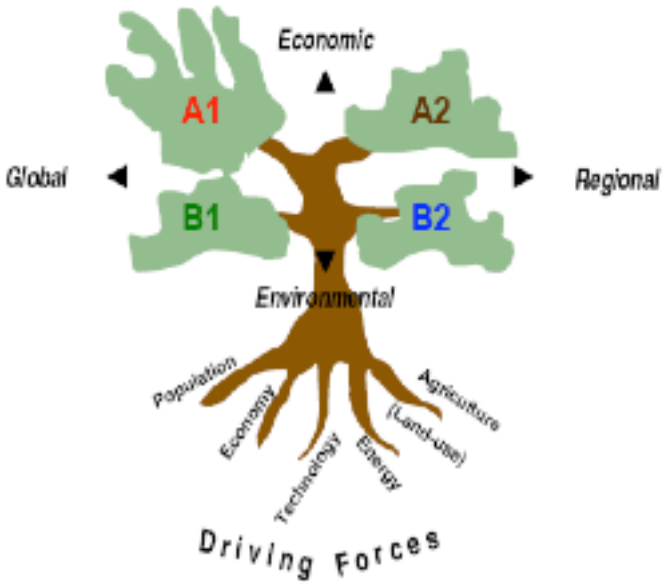

Fig. 3: The four IPCC scenario storylines (A1, A2, B1 and B2) and their relationships with the forces driving greenhouse gas, economic and environmental development and their evolution during the 21st century for large world regions and globally (adapted from IPCC-TGICA, 2007).

1.2 Ecological niche

1.2.1 Definition

The biogeographic assumption that climate exerts a dominant control over the distribution of species is supported by evidences from fossil record to recently observed trends (Walther *et al*., 2002; Pearson and Dawson, 2003; Soberón and Peterson, 2005; Barbet-Massin *et al.,* 2010; Stigall, 2011). The bioclimatic envelop that limit and define the multidimensional space where the species is potentially able to maintain populations is defined as ecological niche (Hutchinson, 1957). These ecological requirements are generally divided into fundamental and realized ecological niches. The former corresponds to the geographic region with appropriate set of abiotic factors (physical and climatic conditions) that impose physiological limits on species' ability to persist in an area (Peterson *et al.,* 1999; Pearson and Dawson, 2003). The later was defined as a subset of the fundamental niche (Hirzel and Le Lay, 2008). Thus, the realized niche incorporates abiotic conditions, the effects of interactions with

other species (biotic factors), and competitive exclusion (Guisan and Zimmermann, 2000; Peterson and Vieglais, 2001; Pearson and Dawson, 2003; Soberón and Peterson, 2005). Quantifying differences between the fundamental and the realized niche of a species, from a geographical point of view, are particularly important because they allow distinguishing whether a distribution is predicted from theoretical physiological constraints or rather from field derived observations (Guisan and Zimmermann, 2000), and also for describing and understanding niche dynamics (Pearman *et al.,* 2007). However, the notion of equilibrium within ecological niches has become increasingly suspect because of species' dispersal and environment variability (Hirzel and Le Lay, 2008). Thus, a species will be geographically present where both ecological factors described before were positively combined with area that is within the dispersal capabilities of the species in question, either in the present day or through the relevant past (Soberón and Peterson, 2005; Hirzel and Le Lay, 2008; Peterson, 2011). The combination of biotic factors, abiotic factors and movement factors delimit geographical distributions of species (Fig. 4 - the 'BAM' (biotic, abiotic, movement) diagram) (Peterson, 2011).

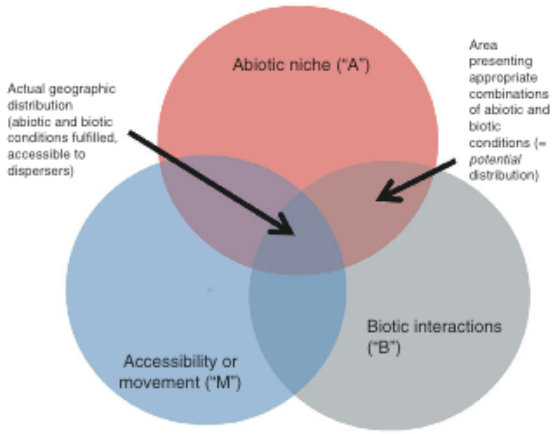

Fig. 4: The "BAM diagram", showing a simplified framework for understanding where species will and will not be distributed. Distributions of species are seen as responding to three sets of factors: the abiotic niche or fundamental ecological niche (A) and the biotic niche (B), and the realized ecological niche (A ∩ B, here termed the potential distribution). "M" for movement, is composed of those ecological parts accessible to the species, without barriers to movement and colonization. The intersection of A ∩ B ∩ M represents the region that has the right set of biotic and abiotic factors and that is accessible to the species.

Several studies have proposed slow changes of species niches under natural selection over evolutionary time periods, "niche conservatism" (Peterson *et al.,* 1999; Peterson, 2011). This stability of the species fundamental niche was predicted based on diverse studies that identified rates of adaptation in ecological niches slower than extinction processes (Peterson *et al.,* 1999). The concept of "niche conservatism" has been variously defined as similarity between sister species, similarity in a species'

niche parameters through time and space, and stasis in a species' niche parameters through time (Peterson *et al.,* 1999; Pearman *et al.,* 2007; Stigall, 2011). To prove the existence or not of niche conservatism, results from paleo-modeling with genetic data were compared (Peterson *et al.*, 1999). However, evidence for ecological niche conservatism is mixed (Martínez-Meyer *et al.,* 2004; Pearman *et al.,* 2007; Peterson, 2011). In general, recent and short-term events (e.g. species invasions, distributional shifts at the end of the Pleistocene) show a considerable tendency towards conservatism, while longer-term events (e.g. differentiation across phylogenies) show increasing degrees of breakdown of conservatism (Peterson and Nyári, 2007; Peterson, 2011). Despite some tendency in the literature towards conservatism (Peterson *et al.,* 1999; Martínez-Meyer *et al.,* 2004; Martínez-Meyer and Peterson, 2006), several examples of non-conservative ecological niche evolution have also been documented (Peterson and Nyári, 2007; Peterson, 2011). However, some of the reported changes on the ecological niche appear to be a consequence of methodological artifacts and model overfitting (Peterson and Nyári, 2007; Peterson, 2011). The diverse and growing body of evidence supporting the idea of ecological niche conservatism offers a considerable potential for prediction and forecasting of biodiversity phenomena (Peterson *et al.,* 1999; Peterson, 2006, 2007; Peterson and Nyári, 2007; Stigall, 2011).

1.2.2 Ecological niche-based modeling

The evolution of modeling strategies (as we know today) started when the new statistical methods from field-based habitat studies were linked with Geographical Information System or GIS tools. Early studies were dedicated to describe biological patterns and their connections with geographical and environmental gradients (Elith and Leathwick, 2009). Currently, they have become an important instrument to understand species' ecological requirements and to recognize aspects of biogeography, evolutionary phenomena, and more recently, to assess the impacts of global biodiversity threats, such as fragmentation and climate change (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Araújo *et al.,* 2005; Thuiller, 2007; Barbet-Massin *et al.,* 2010). Attempts to address some of these biodiversity issues have relied on the species-climate "envelope" modeling approach, also known as ecological niche-based models (ENM) (Pearson *et al.,* 2006). The ENMs relate known occurrences of species to a series of environmental variables, predicting the suitability of the habitats across the landscape in the present, past and future (Araújo, *et al.,*

2005; Araújo and Rahbek, 2006; Waltari and Guralnick, 2009; Pearman *et al.,* 2010; Warren *et. al*., 2010). These predictions are based on the assumptions of niche conservatism and that species' distribution is mainly determined by the environment, and not by other factors such as competition or predation (Waltari and Guralnick, 2009).

Whilst the modeling approach is generic, different techniques have been employed to define potential ranges. The impact that the specific method has on model predictions is an important consideration in model applications (Pearson *et al.,* 2006). Multiple methods have been developed according to different algorithms and particularly species data requests. The regression-based models, such as generalized linear model (GLM), are widely used by ecologists to predict species distribution with presence/absence data (Guisan *et al.*, 2002; Elith and Leathwick, 2009). The GLMs model the variation in species occurrence or abundance within the occupied environmental space selecting predictors according to their observed importance (Elith and Leathwick, 2009). They are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables (Guisan *et al*., 2002). Their ability to deal with complex data types, including abundance data with many zeros, records with imperfect detection of presence, and structured samples of data, make them more flexible and better suited for analyzing ecological relationships (Guisan *et al.,* 2002). However, absence data are usually poorly available (Phillips *et al.,* 2006) and it is easily misidentified. Despite the recognition of the robustness of presence/absence data, their sampling is a crucial part of the process and it should be unbiased to be representative of the whole population. Absence data are particularly difficult to obtain accurately and can be easily misleading by the absence of detection of the species (even though it was present), absence of the species for historical reasons (even though the habitat was suitable) or absence of the species for geographical (inaccessibility) despite the suitability of the habitat. In fact, only habitat unsuitability is relevant for the predictors but "false absences" can easily bias the analyses (Guisan *et al.,* 2002; Elith and Leathwick, 2009). Given the general scarcity of absence data, researches often resort to modeling techniques that require only presence observations as input data. The Ecological Niche Factor Analysis (ENFA) is a presence-only modeling approach. It computes suitability functions by comparing the species distribution (presence data) in the ecogeographical variable space with that of the whole set of cells (Hirzel *et al.,* 2002). Like the Principal Component Analysis, ENFA summarizes all predictors into a few uncorrelated factors

retaining most of the information. However, in this particular case, factors have an ecological meaning: the first factor, “marginality”, reflects the direction in which the species niche mostly differs from the available conditions in the global area. And the second factor “specialization” represents the breadth of the niche space of a species. A large part of the information is accounted for by a few of the first factors. The species distribution on these factors is used to compute a habitat suitability index for any set of descriptor values (Hirzel *et al.,* 2001, 2002). Some pitfalls applied to presence–absence dataset modeling may also affect the accuracy of presence-only modeling. For instance, the number of occurrence localities used to estimate the parameters of a model is frequently too low, compromising reliability (Philips *et al.,* 2006). Because of sample size limitations, Maxent is a general-purpose method for making predictions or inferences from incomplete information. It is based on the Maximum Entropy algorithm that estimates the distribution of a species by finding the probability distribution of maximum entropy, i.e. closest to uniform (Philips *et al.,* 2006; Araújo and New 2007; Elith *et al.,* 2011). More recently, the artificial neural networks (ANNs) have been increasingly applied to biological systems because of its ability to deal with complex datasets (Tarroso *et al*., 2012). The ANNs can identify and learn correlated patterns between input data sets and corresponding target values, making powerful tools for models, especially when the underlying data relationships are unknown (Lek and Guégan 1999).

1.2.3 Applications and limitations

The use of Ecological Niche Models (ENM) to model niches into new regions and scenarios of future climate change enables the geographical distributions of suitable conditions to be predicted. Whilst the modeling approach is generic, studies have employed a number of different techniques for defining potential ranges and the impact that the specific method has on model predictions is an important consideration in model applications (Thuiller *et al.,* 2004: Pearson *et al.,* 2006). The use of ENMs for applications such as conservation planning creates an imperative for considering errors and uncertainties. The decision of which model to use has generally been ad-hoc, and there is little consensus regarding the relative performance of ecological models (Araújo and Rahbek, 2006). In fact, the variability between predictions from alternative models have been demonstrated, showing that the selection of the modeling technique to address a particular question is a very important part of the modeling process and that has a huge impact on results (Pearson *et al.,* 2006). Studies have reported that projections arising from species models may be highly sensitive to the assumptions,

algorithms and parameterizations of different methods raising a number of methodological issues that lead to a degree of uncertainty (Araújo *et al.,* 2005). Furthermore, the ENMs are based in the assumption of ecological niche conservatism, discarding adaptability, capacity to persist in refugia, and adaptation to suboptimal future environmental conditions. Models are based on some problematic ecological assumptions, such as that species distribution and assemblages are in a constant steady-state relationship with contemporary climate that, despite being clearly acknowledge, remain unresolved (Araújo and Rahbek 2006). In fact, during the past millions years, species range expanded and contracted due to climate oscillations, adjusting their needs to always changing environmental conditions, leaving open the possibility of adaptation to suboptimal future environmental conditions. One critical question is whether models that can successfully predict current species distributions also provide robust predictions of future distributions under climate change. Different bioclimatic models can produce highly variable predictions of species-range shifts, and there is a poor correlation between a model's ability to fit present and future distributions. Evaluating model performance under climate change requires a paradigm shift, because there are no data against which predictions of future ranges can be tested (Araújo and Rahbek, 2006). In the context of climate change, uncertainty in projections becomes even more worrying as additional sources of variability arise at two levels with the use of future climate scenarios. Firstly, a large number of general circulation models (GCM) have been developed simultaneously to simulate the response of the global climate system to increasing greenhouse gas concentrations. The variability regarding different GCM has been documented to be larger within the same time period than across periods adding some uncertainty to the modeling process. Secondly, four storylines, which are alternative images of how the future might unfold assuming a certain level of future greenhouse gas emissions, have been defined are derived from a complex interplay between demographic and socio-economic developments, as well as technological changes. Uncertainty due to GCMs could therefore be as large as uncertainty due to SDM at the end of the 21st century (Buisson *et al.,* 2010; Maiorano *et al.,* 2012)

One of the critical issues for making projections of species distributions into different spatial or temporal scenarios is to have appropriate descriptions of species realized niches. Realized niches are commonly approximated by series of curves describing the likelihood of species' occurrence following a set of environmental predictors using presence/absence or abundance data. One of the problems with this

procedure is that modelers often lack information on the overall species potential or realized distributions. Hence, response curves are often incomplete descriptions of the responses of species to environmental predictors. The consequences of such loss of information (species' climatic space) by modeling partial niches may be reflected on the under-estimation of potential distribution when projected across time or space (Thuiller *et al.,* 2004)

1.3 Threatened African mega-fauna

The African continent warming throughout the last 100 yr has been about 0.5°C. Predictions for the future suggest that the continent on average could be between 2 and 6°C warmer by the end of the 21st century (Hulme *et al*., 2001). Additionally, the uncertainties around the predictions of future changes in rainfall (Hulme *et al*., 2001) place the African continent as highly vulnerable to the 21st century climatic changes (Garcia *et al.,* 2012). Forecasts of changes in climate above the global average projected to Africa and the combination with illegal wildlife poaching and habitat fragmentation will likely increase range contraction and species extinction (Brooks *et al.*, 2002; Pimm, 2008; Garcia *et al.,* 2012). Africa is a vast and exotic continent with an abundant wildlife resource of unique value but the variety and abundance of wildlife in Africa is shrinking fast as human populations grow and invade wild land. With the beginning of the 20th century and the increasing human pressure, particularly poaching, large-sized species range contracted and many peripheral populations were extirpated (Lindsey *et al.,* 2013)

1.3.1 Savannah elephant (*Loxodonta africana*)

The African elephant (*Loxodonta africana*, Blumenbach, 1797) is the largest terrestrial mammal living on Earth and the symbol of African continent. Until recently, two subspecies were included in this taxon. However, Roca *et al.* (2001) based on genetic, morphological and ecological data, proposed the division of both and the recognition of species-level between African elephant groups. Further studies (Comstock *et al.,* 2002; Ishida *et al.,* 2011) have added evidence supporting these conclusions but the recognition of the Savannah elephants and the Forest elephant (*L. cyclotis*) as distinct species is far from being a consensus in the scientific community (Blanc *et al.,* 2007). Here, we assume the division proposed by Roca et al. (2001) and only evidences from the Savannah elephant were considered.

The Savannah elephant (hereafter "elephant") is a "keystone" species that plays a pivotal role in structuring both plant and animal communities (Blanc *et al.,*

2007; Kohi *et al.,* 2011). It ranges from the sub-Saharan region to the south of the African continent, excluding the African tropical forest in the central region (Roca *et al.*, 2001; Comstock *et al.,* 2002; Ishida *et al.,* 2011). However, the distribution is not continuous and in the past few decades, it has become increasingly fragmented and it is known to have become nationally extinct in some countries during the 20th century (Barnes, 1999; Blanc *et al.,* 2007). The IUCN recently changed the classification of African elephants (both species considered) to VU (Vulnerable A2a – estimations of population size reduction of ≥ 30% over the last 10 years or three generations) but the status of African elephants varies considerably across the species' range (IUCN, 2012). Western elephant populations have been particularly butchered and the distribution has been reduced to tiny scattered fragments and is nowadays classified as threatened (Cumming *et al.,* 1987; Barnes, 1999, 2002; Blanc *et al.,* 2007). On the other hand, southern populations are currently increasing and are considered as least concern (Blanc *et al.,* 2007; Bouché *et al.,* 2011).

The African elephant is one of the most notorious species of the African continent. Records from European travelers and explorers in the beginning of the 20th century (and even earlier) had already registered species presence, population distributions and extinction, and more frequently hunting episodes (Boyd, 1907; Wildfred, 1939; Gowers, 1948; Lee and Graham, 2006). The species has a long history of human disturbance. Directly or indirectly, humans have been shaping populations and species' range, through habitat fragmentation, illegal hunting and trading, and climatic change (Lee and Graham, 2006; Archie and Chiyo, 2012). Historical demands for ivory among early civilizations go back to the 4th century AD. Few centuries later, Europe was importing c. 100–200 tons of ivory per year and by the late 19th century, European ivory imports may have reached 700 tons, representing a potential 60,000 elephants killed per year (Naylor, 2004; Lee and Graham, 2006). During the last century, the availability of modern weapons and road development has made it far easier for people to kill large mammals and by the middle of the 1970s a pick of ivory demand threw elephants' populations to instability (Cumming *et al.,* 1987; Lee and Graham, 2006; Bouché *et al.,* 2011; Archie and Chiyo, 2012). After CITES banned ivory trade in 1989, elephant populations recovered substantially over much of central, eastern and southern Africa, although they have never recovered to their pre-poaching levels (Stiles, 2004; Lee and Graham, 2006). Presently, studies do not indicate any major continental decline rather showed a significant increase in the number of elephants, particularly in southern protected areas (Lindsey *et al.,* 2013; Douglas-Hamilton, 2009). Despite this general populations' trend, recent reports pointed to a

dramatically increase of poaching, asserting that the rate of illegally killed elephants is worse than it has ever been before (Douglas-Hamilton, 2009; Lindsey *et al.,* 2013). This trend in elephant poaching is apparently fueled by demand in Asia, the rise in the price of ivory and proliferation of illegal uncontrolled markets (Naylor, 2004; Douglas-Hamilton, 2009; Lindsey *et al.,* 2013). Wildlife products and particularly ivory, are sold or bartered for food, arms and ammunition (Chase and Griff, 2011). Furthermore, civil wars and political instability add an extra pressure to populations already repressed by poaching (Naylor, 2004; Chase and Griff, 2011; Lindsey *et al.,* 2013). The effects of illegal hunting and trading on elephant societies and genetic structure are beginning to be studied and major consequences in reproduction and diversity loss are already expected (Archie and Chiyo, 2012).

Wild elephants are also facing new threats from habitat fragmentation and human-wildlife conflict to climate change (Archie and Chiyo, 2012). Almost everywhere where elephants live, there is an ever-expanding, resource-hungry human population and elephants are increasingly being constrained to live in smaller areas (Douglas-Hamilton, 2009; Archie and Chiyo, 2012). Humans settled on land formerly occupied by wildlife and elephants, closing off old migration routes and corridors to neighboring refuges, restricting the range of elephants and fragmenting habitat, increasing the conflict between humans-elephants (Hema *et al.,* 2010). The land use transformation has a major impact on species that are trying to cope with changes in climate. Although predictions for elephants under climate change show a trend of future expansion of the suitable area, current protect areas are likely to become less suitable for the species presence (D'Amen *et al.,* 2013).

Elephants have been the focus of intense conservation studies and debate for a long time, particularly as their numbers have decreased by nearly 50% in the 1980s (Comstock *et al.,* 2002). Although elephants have been listed as vulnerable and protected since 1989, illegal poaching and habitat destruction continue to diminish and isolate remaining populations. The impacts of human beings will probably reverse the predictions of expansion in suitable habitat and consequent population growth. In fact, studies refer the rapid growth of an elephant population under good environmental conditions after being released from the stress of heavy illegal hunting (Foley and Faust 2010). As the largest land mammal, the savanna elephants should be hard to miss, making them ideal for modeling studies. Furthermore with the existence of a long historical presence record and interactions with humans, becomes possible to address

the effects of poaching, habitat fragmentation and climate change in both partial and full niche.

1.3.2 Giraffe (*Giraffa camelopardalis*)

The giraffe (*Giraffa camelopardalis* Linnaeus 1758) is one of the most emblematic and popular species in the African continent. Within the last century, numerous taxonomic schemes have been developed to reflect the regional differences in pelage pattern and morphology (Brown *et al.,* 2007; Fenessy and Brown, 2010). Several studies have proposed taxonomic classifications ranging from the recognition of two species to ten subspecies (Brown *et al.,* 2007). The uncertainty surrounding the geographic and taxonomic limits of all giraffe subspecies have been debated and in part reflects the high variability in pelage patterns within some populations and suspected hybridization among putative subspecies (Brown *et al.,* 2007; Fenessy and Brown, 2010). Currently, the IUCN recognize only two subspecies belonging to a single species *G. camelopardalis*, the *G. c. peralta* from West Africa (Hassanin *et al.,* 2007) and the *G. c. rothschildi* from Central Africa (Brown *et al*., 2007*)*

Formerly, giraffes occurred in a wide region of the sub-Saharan Africa but nowadays the range has dramatically contracted and fragmented (especially in West Africa) to small populations scattered throughout the southeast Africa (Fennessy and Brown, 2010). Since the beginning of the 20th century, the density and distribution of giraffe populations has decreased across the entire continental to a total of c.140,000 by the late 1990s and currently to 80,000 (Suraud *et al.,* 2012). The IUCN classification listed giraffes provisionally as Least Concern. However, recently surveys suggested a decline in the total population, placing the hypothesis of listing it in a higher category of threat (Fennessy and Brown, 201). While some populations remain stable or are even increasing, others are clearly in a more precarious position and may well be threatened (Fennessy and Brown, 2010), particularly those in West Africa (Suraud *et al.,* 2012).

The distribution of the giraffe until the beginning of the 20th century has essentially depended on the climate, suitable vegetation and permanent water sources, and its range extended throughout northern Africa (Ciofolo, 1995; Suraud *et al.,* 2012). By the end of the 19th century, the giraffe was present across the Sudano-Sahelian zone from Chad to Senegal and only natural geographical barriers kept the species from colonize new areas (Ciofolo, 1995). The turn of the century marked the start of the species decline. The introduction of firearms allowing extensive hunting, the developments of agriculture, the deforestation, and the construction of railroads led to

population declined and range contraction, being now extinct in most places that otherwise would not be (Ciofolo, 1995; Fennessy and Brown, 2010). Giraffes are mainly poached because of their tails meat and hide. Tails are highly prized by many African cultures and are sold to make bracelets and fly whisks. Despite the implementation of an anti-poaching program in the early 1980s, the number of giraffes continued to decline (Suraud *et al.,* 2012). Future changes in climate will enhance the consequences of these threats, forcing species to contract or move their ranges. In the case of the giraffe, future predictions show a tendency to range contractions (D'Amen *et al.,* 2013). Populations from East Africa are expected to extent their suitable habitat, on the other hand, future predictions for southern populations reveal major losses, particularly in Angola and Namibia (D'Amen *et al.,* 2013).

The giraffe is a well know species and records from its presence go back to the beginning of the 20th century, when the first European explorers reported population distribution and hunting scenes (Boyd, 1907). Long historical records give the opportunity to address the consequences of illegal hunting and land transformation. Furthermore, as the tallest species living on Earth, false absences are unlikely, making this species ideal to test modeling approaches, and consequences on full and partial niche modeling.

2. Objectives

Compare the effects of using partial niches for the predictions of future species' distributions due to climate change. For this, we will use current and historical distributions, assumed to represent the partial and full niche, respectively. In parallel, we will test four modeling approaches regarding their sensitivity to climate change predictions using both presence datasets. Savannah elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*) will be used as case-studies, given their long historical records, reliable presence/absence data, and indication of population fluctuations due to interactions with humans' activities. Modeling historical and current distributions will also allow inferring the effects of human activities during the 20th century on the range and ecological niche of these species under current and future climatic conditions. More specifically, the aims of this thesis are to:

1) Assess niche shifts under human activities since the beginning of the 20th century;

2) Test for differences between modeling approaches and their ability to predict suitable areas for both periods;

3) Estimate changes in modeling predictions and occupied niche between historical and present distribution;

4) Estimate range shifts under climate change, considering the historical (full niche) and current distributions (partial niche).

Results from this study are expected to act like a cautionary tale when using blindly data for current species distributions to predict their future ranges due to future climate change. The calculation of partial-niche models may lead to severe underestimations and undermine the effectiveness of conservation measures to respond to climate change challenges. Consequently, it is expected that this study may offer new insights and guidelines for the methodological approach of estimating species distributions in response to predicted climate change.

3. Methods

3.1 Study area

The African continent (discarding islands) was selected as study area once it corresponds to the global distribution of the target species (Blanc, 2008; Fennessy and Brown, 2010).

3.2 Species and distribution data

A total of 1061 and 438 observations of elephants and giraffes, respectively (Tab. 1), were gathered from bibliographic references (available as supporting information, List S1). These included localities with geographic coordinates or with clear toponomies from which it was possible to gather coordinates from Google Earth to a precision of 20km. Observations were collected from late nineteenth century until the present. Two presence datasets were created for each species (available as Fig. S1): the first one corresponding to the current distribution of the species (hereafter Present), and the second one corresponding to the distribution at beginning of the 20th century (hereafter 1900). The 1900 dataset was created comprising all the data from Present and adding the locations were the species are currently extinct. Historical observations were contrasted with the present distribution available at IUCN (Blanc, 2008; Fennessy and Brown, 2010) Observations (species level) falling outside IUCN polygons were considered as extinct localities.

Each presence dataset was divided into two subsets for training and testing models. Observations for the training dataset were selected from clusters of species occurrence in a grid of 100x100 km. The Nearest Neighbor Index (NNI) given by the Geographical Information System (GIS) ArcGIS 9.3 (ESRI 2009) was used to assess the degree of presence data clustering. NNIs of 1900 and Present training datasets indicated random distribution for the elephant, 0.759 (p=0.000) and 0.720 (0.000), respectively, and for the giraffe, 0.869 (p=0.001) and 0.879 (p=0.072).

Table 1 – Datasets of elephant and giraffe observations used in models of current (Present) and early past distribution (1900), discriminating training and test subsets.

		Training	Testing	Total
Elephant	1900	283	475	758
	Present	144	159	303
Giraffe	1900	169	134	303
	Present	61	74	135

To quantify prediction biases in SDMs, we randomly generated pseudo-absence datasets with the same number of observations used in the training datasets. Random absences were created outside buffers encompassing the presence dataset of each species in each time period. Buffer size was set according to home range size estimations for both species: 300km (Fennessy, 2001, 2009; Roever *et al*., 2012; Wall, *et al*. 2013) around each observation.

3.3 Environmental factors

Environmental factors such as primary productivity, water availability and seasonal variation of temperature and precipitation are thought to limit ranges of terrestrial mammals (Hawkins *et al*., 2003). A set of 11 environmental factors, or ecogeographical variables (EGVs), was selected according to their meaning to the ecology and distribution of the model species. These included two topographical grids, terrain ruggedness index (hereafter TRI) and altitude and nine bioclimatic grids (available as Tab. S1). Accordingly, nine bioclimatic variables available in WorldClim website (Hijmans *et al*., 2005; http://www.worldclim.org/) were selected to represent averages, variability, seasonality and environmental extremes of these factors. Additionally, two topographical grids (TRI and altitude) were considered to evaluate the existence of dispersal barriers. The TRI was calculated by defining the mean difference between a central pixel and its surrounding cells (Wilson *et al.,* 2007).

Predictions of future climates were obtained from WorldClim from four Global Circulation Models (CCCMA, HadCM3, CSIRO and Nies99) under two IPCC 3th Assessment emission scenarios (A2a and B2a) for the 2080 time period (Hijmans *et al*., 2005). Different scenarios were chosen according to different potential impacts of different assumptions with respect to demographic, socio-economic and technological development on the release of greenhouse gases. All EVGs were downloaded from Worldclim and upscaled to 0.18 degrees, approximately 20 kilometers.

3.4 Modeling strategy

Analyses were done based on an attempt to account for uncertainties related to different modeling algorithms. Four different species distribution models were developed using identical input variables and datasets to simulate current and potential future distributions.

1) Ecological-Niche Factor Analysis (hereafter ENFA) was performed using Biomapper 4.0 software (Hirzel *et al.,* 2001, 2002a,b;

http://www2.unil.ch/biomapper/enfa.html). ENFA compares the distributions of the EGVs values between the species occurrence dataset and the whole study area, summarizing all the EGVs into new uncorrelated factors with ecological meaning (Hirzel *et al*., 2002a). Presence datasets of the target species and the EGVs were converted into Idrisi-formatted maps. A covariance matrix was performed to check EGVs variability and then models using 1900 and Present datasets for both species were created. Niche breadth parameters as marginality (ecological distance between the species optimum and the mean habitat within the reference area) and specialization, (the ratio of global variance to species variance – niche breadth) were taken from each ENFA output. The outcome models depict suitability scores of each pixel for species presence.

2) Generalized Linear Models (hereafter GLM) based on logistic regression resorting to R software (http://www.r-project.org/) was used to predict species distribution. From this modeling approach results a single formula, where each coefficient multiplies its related predictor variable (Guisan *et al*., 1999, 2002). The model was then implemented in the GIS and maps were produced. The outcome had finally to be transformed by the inverse logistic function to be scaled between 0 and 1. Values of significance of variables for model building were extracted from the output and a single model was generated for each species x time period.

3) Maximum Entropy principle (hereafter Maxent) was applied with Maxent 3.3.3 kappa version software (Phillips *et al*., 2006; Phillips and Dudík, 2008; http://www.cs.princeton.edu/~schapire/maxent/). Two average models were developed for each species resulting from 50 replicates for each model type using random seed, Observations for each replicate were chosen by bootstrap allowing sampling with replacement in each model replicate. Presence data were randomly chosen as test data (20%) for each model. The output models were obtained in probability of occurrence and resulted from an averaged of the 50 replicates. As a measure to model fitness we used the area under curve (AUC) of the receiver-operating characteristics (ROC) plot.

4) Artificial Neural Networks (ANN) (Lek and Guégan, 1999) were derived SIMAPSE software (Tarroso *et al.,* 2012; http://purl.oclc.org/simapse). As a powerful modeling tool, able to deal with complex ecological datasets, the ANNs have been increasingly applied in biological field in the last decades (Lek and Guégan, 1999). This methodological approach combined with SIMAPSE software builds several models with different sub-sampling, creating a final average prediction and taking into account the

independent information of the individual models and a description of uncertainty between individual models (Tarroso *et al.,* 2012). As input was used a dataset of presence-absence, as sub-sampling method was chosen bootstrapping and for each model type was done a set of 50 replicates. All other parameters were set to the application's default. The AUC value was used as a fitness measure was extracted from the model output with the lowest error.

To the resulting models of each species X dataset combination, considering the four different modeling approaches, was applied a threshold to classify continuous probabilities (exception for ENFA where outcome models are obtained in suitability scores) into presence-absence scores. Thresholds were selected individually based on the value that minimizes the difference between sensitivity (the probability that the model will correctly classify a presence) and specificity (probability that the model will correctly classify an absence) (Liu *et al*., 2005). The correct classification rate was calculated for training and test datasets by intersecting presences with their respective binary SDM and used as model fitness measure for all approaches. Values were converted in percentages.

Models were designed according to each modeling approach described above for both species considering two time periods. A total of 16 SDMs were projected to 2080 for each Global Circulation Model (CCCMA, CSIRO, HadCM3 and Nies99) and emission scenario (A2a and B2a), resulting in 128 simulations in total. Before applying thresholds, consensus maps for predictions were created. Thus, probability of presence maps (suitability scores in ENFA), were combined in order to create a single prediction for each species dataset and modeling technique. Spatial standard deviation between GCMs (within each modeling approach) and between modeling procedures were estimated in order to be possible to identify disagreement areas. Thresholds previous calculated were applied to future predictions and maps of probability of occurrence were converted into presence/absence.

Consensus maps for current and early past distribution were created for all four techniques from an ensemble of binary models considering species and time period. The outcome distribution models were then reclassified into two classes (0/1) using middle values as threshold (each pixel was only considered suitable if at least half of the models classified them in the same way). The same procedure was used in models for future predictions. Binary models were combined by species dataset and emission scenario. A single model was created per modeling tool for 2080.

3.5 Statistics analysis

3.5.1. Importance of EGV

The importance of EGVs for explaining species distribution was determined by four different parameters regarding each modeling approach. In ENFA, the scores of the first axis were used as measure of EGVs contribution to distribution models. The first axis (or factor) is the one that maximizes the explanation of the species distribution and is also known as marginality. The higher the absolute value of a coefficient, the further the species departs from the mean available habitat regarding the corresponding variable. In other words, positive coefficients indicate preference for locations with higher than the mean values on the corresponding EGV available in the study area, whereas negative coefficients show that the focal species prefers values that are lower than the mean (Hirzel *et al*., 2002; Hirzel and Le Lay, 2008). Significance levels and signs of the coefficients of each EGV in the GLM models were taken as an indication of the importance of each EGV to the model and the relationship between species occurrence and each EGV, respectively. In Maxent, the importance of EGVs for explaining species distribution approach was determined from their average percentage of contribution to each training model. Species occurrence and EGVs relationship was determined by visual examination of response curves profiles from univariate models. In Simapse, the sensitivity of the network to the input data was measured using the partial derivatives algorithm (PaD). This acts by setting all variables to zero except one, for which it depicts the predictive behavior throughout its range of values. From the outputs, it was extracted: (i) the variables contribution to the model; and (ii) the individual partial derivatives that measure the sensitivity throughout each variable range (Tarroso *et al*., 2012).

3.5.2 Spatial agreement between models

Map comparison methods were used to detect temporal/spatial changes in suitable areas using the Map Comparison Kit software (Visser and Nijs, 2006; http://www.riks.nl/mck/). A kappa analysis was performed to assess spatial agreement between modeling tools considering individually the beginning of the 20h century, present and respective predictions to the future. The same analysis was performed between emission scenarios, according to each dataset.

3.5.3 Temporal changes

Temporal changes were inferred using ArcGIS 9.3 among consensus binary models of all time periods. Present maps were compared to 1900 assuming thereby that the species distribution in that time period represented the full niche. The number of suitable pixels for each presence map was quantified and differences between time periods were estimated. To evaluate niche evolution, presences values extracted from two of the most explicative EGVs, for the early past and present, were plotted for the elephant and giraffe.

4. Results

4.1 Models evaluation

The values of AUCs exhibited high average for Maxent and Simapse modeling techniques, for both training and test datasets (ENFA and GLM do not produce this information). In Maxent, the average AUCs for training datasets ranged from 0.80 to 0.93 between both species, whereas for Simapse the average AUCs for training datasets varied from 0.80 and 0.91 (Tab. 2). The correct classification of presences revealed a great modeling performance with values ranging from 69.2 to 97.9 in training datasets and from 63.5 to 97.0 in test datasets (also available in Tab. 2).

4.2 Environmental factors

Measures of variable contribution indicate that the most important EGVs related to the distribution of both species were identical to all model approaches. Overall, the range of elephants was mostly related to temperature seasonality (BIO 4), annual precipitation (BIO 12) and precipitation in the wettest month (BIO 13) either for 1900 or Present distribution models. The same three EGVs were related to the range of giraffes, however, particular differences were found between modeling approaches (see Tab. 2).

	Elephant							
	1900				**Present**			
	ENFA	GLM	Maxent	SIMAPSE	ENFA	GLM	Maxent	SIMAPSE
Temperature Seasonality (BIO 4)	**-0,488**	**0,000**	**0,53**	**44,5**	**-0,477**	**0,000**	**0,53**	36,5
Annual Precipitation (BIO 12)	0,190	**0,000**	**0,51**	**36,3**	0,257	**0,000**	**0,70**	**50,1**
Precipitation of Wettest Month (BIO 13)	**0,412**	**0,000**	0,39	17,8	**0,467**	**0,000**	0,49	**43,9**
Precipitation Seasonality (BIO 15)	0,385	**0,000**	0,27	27,4	0,312	0,100	0,36	33,1
Max Temperature of Warmest Month (BIO 5)	-0,291	1,000	0,10	9,5	-0,295	1,000	0,16	18,1
Precipitation of Driest Month (BIO 14)	-0,157	1,000	0,03	16,4	-0,117	1,000	0,03	19,1
Altitude	0,267	1,000	0,09	21,7	0,115	1,000	0,11	12,5
Annual Mean Temperature (BIO 1)	0,006	0,001	0,06	16,3	0,043	0,100	0,10	16,4
Min Temperature of Coldest Month (BIO 6)	0,205	0,050	0,12	8,3	0,275	1,000	0,14	11,9
Temperature Annual Range (BIO 7)	-0,339	1,000	0,40	7,3	-0,394	1,000	0,40	3,3
Ruggedness	0,265	1,000	0,07	4,5	0,211	0,050	0,07	6,0
CCR Training %	74,9	92,6	97,9	93,3	75,7	80,6	95,1	90,3
CCR Test %	76,4	95,8	98,5	94,9	69,2	83,0	87,4	95,0

	Giraffe							
	1900				**Present**			
	ENFA	GLM	Maxent	SIMAPSE	ENFA	GLM	Maxent	SIMAPSE
Temperature Seasonality (BIO 4)	**-0,458**	**0,000**	0,31	**43,2**	**-0,510**	0,500	0,30	**9,6**
Annual Precipitation (BIO 12)	0,039	**0,000**	**0,38**	**65,2**	0,112	**0,000**	**0,50**	8,4
Precipitation of Wettest Month (BIO 13)	0,297	**0,000**	**0,33**	18,6	0,177	0,001	**0,43**	4,3
Precipitation Seasonality (BIO 15)	**0,664**	1,000	0,22	14,7	0,082	0,500	0,17	2,3
Max Temperature of Warmest Month (BIO 5)	-0,094	1,000	0,07	10,6	**-0,482**	1,000	0,21	3,0
Precipitation of Driest Month (BIO 14)	-0,202	**0,000**	0,02	15,5	0,008	1,000	0,05	2,9
Altitude	0,161	1,000	0,05	6,1	0,381	1,000	0,13	**9,6**
Annual Mean Temperature (BIO 1)	0,235	0,010	0,07	22,1	-0,179	1,000	0,06	3,4
Min Temperature of Coldest Month (BIO 6)	0,258	0,050	0,08	11,3	0,184	1,000	0,04	1,2
Temperature Annual Range (BIO 7)	-0,251	1,000	0,25	4,4	-0,448	1,000	0,23	1,7
Ruggedness	-0,001	1,000	0,04	22,9	0,212	1,000	0,10	5,1
CCR Training %	69,2	82,2	95,3	86,4	70,5	78,7	90,2	80,3
CCR Test %	70,9	90,3	88,1	97,0	63,5	94,6	87,8	74,3

Tab 2: Contribution of EGV for each modeling approach according to each dataset: ENFA - the scores of the first axis; GLM - Significance levels and signs of the coefficients; Maxent - average percentage of contribution; Simapse - partial derivatives algorithm; Correct Classification Rate was also measure for each of the combinations and the results are presented in percentages.

4.3 Historical Niche shift

The niche evolution of model species were analyzed by plotting presence values of two of the most explicative EGVs (BIO4: temperature seasonality; and BIO12: annual precipitation) (Fig. 5). The climatic space of both species diminished from 1900 to Present, however it is more evident and accentuated in the case of the giraffe.

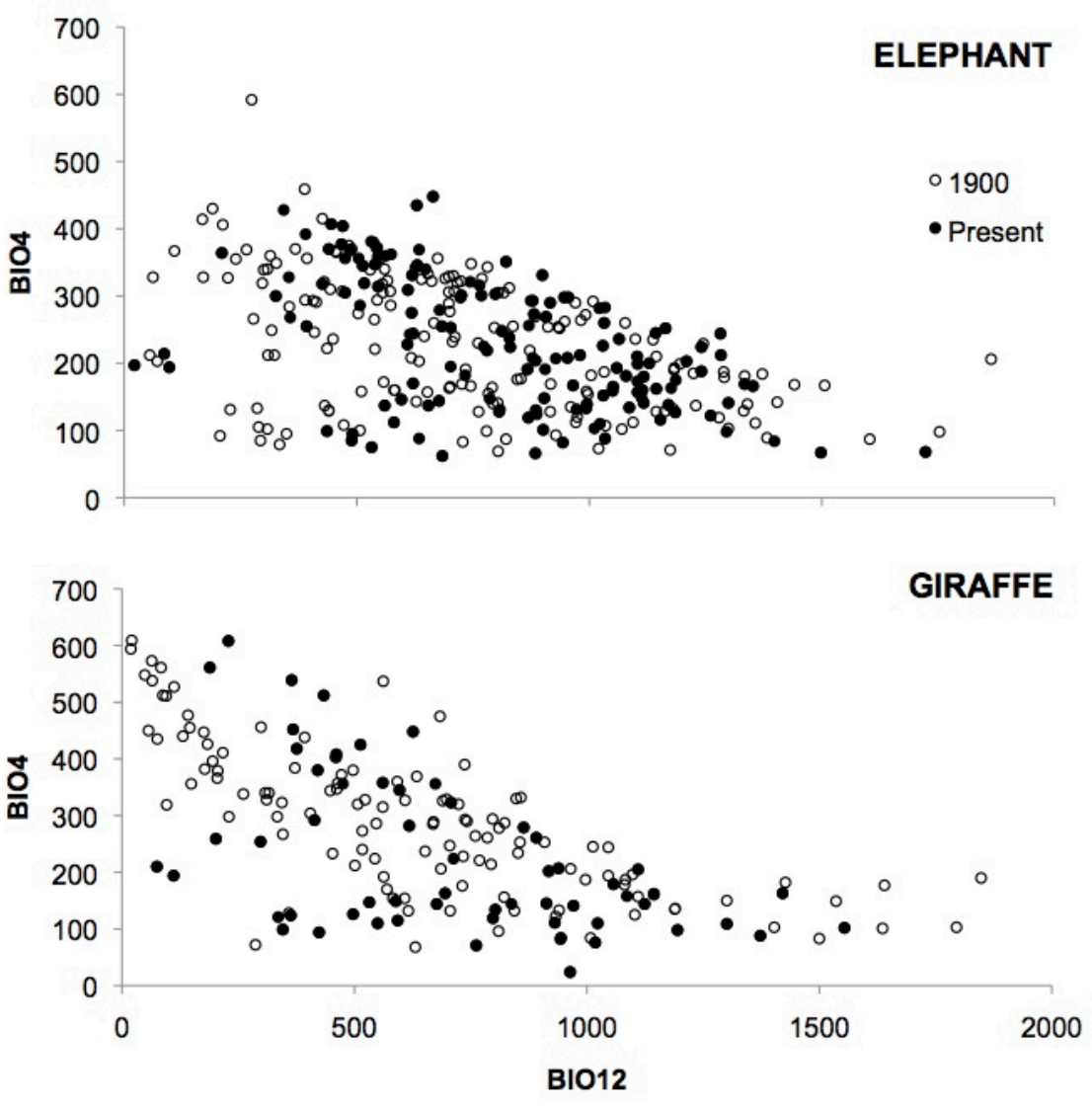

Fig. 5: Plot of presence values of two of the most explicative environmental factors (BIO4 - Temperature Seasonality; BIO12 - Annual Precipitation) for the elephant and giraffe. White dots represent climate distribution in early present (1900) and black dots the current (Present) climate distribution.

In the case of the elephant, marginality increased from 1900 to Present in the elephant models, however tolerance decreased markedly since the beginning of the 20th century (Fig. 6). In the same way, giraffe's marginality increased from 1900 to Present, however, tolerance had a small decline since 1900.

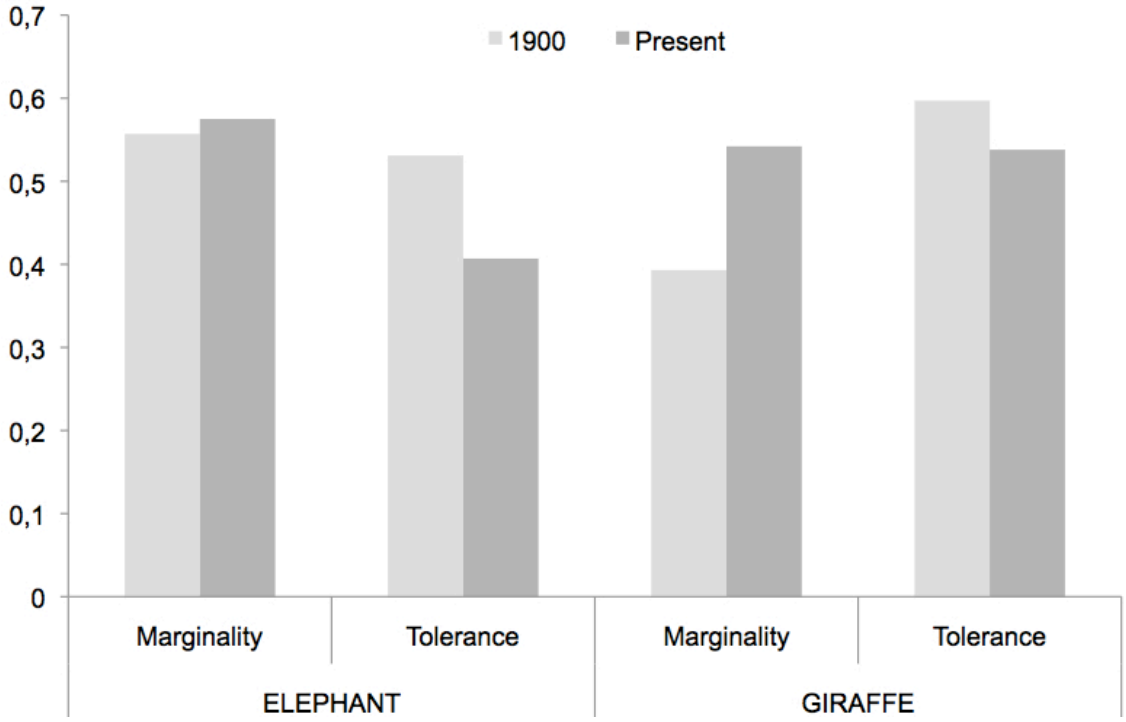

Fig. 6: Marginality and tolerance scores derived from ecological-niche factor analysis for elephant and giraffe according 1900 and Present.

4.4 Differences between models

Standard deviation between models of probability of occurrence (consensus maps) was mapped in order to identify the most inconsistence areas of occurrence (see Fig. S2). Results reveal that marginal regions are more variable and this applies to all datasets and predictions. Models created using ENFA approach demonstrated to have a major influence on these dissimilarities.

Analyses using kappa algorithm were made to infer major differences between modeling tools. Overall, agreement rates between the 1900 and Present models for both species ranged from moderate to substantial. Current and recent past distribution models showed consent between modeling approaches with the exception for ENFA that presented some dissimilarities and the lowest spatial agreement values (see appendix Tab. S3 and Fig. S2). Results obtained from Present dataset revealed major

differences and no common pattern was found between the four modeling tools resorting current models or to predictions under Present dataset (see Fig. S2). Kappa analyses were also made to compare both scenarios A2a and B2a and the results showed that all maps generated were very similar. Values ranged from 0.880 and 0.953 for the elephant and from 0.661 to 0.952 in the case of the giraffe.

4.5 Suitability change under human activities

Spatial distribution of suitable habitat of both model species changed since the beginning of the 20th century (Fig. 7). From an overview, the elephant's distribution contracted, especially in marginal areas and in some other regions it became extremely fragmented. In West Africa suitable pixels almost disappear and in the East and the South region, locations that were classified as suitable for the elephant in the early 1900s, sifted to small and sparse suitable areas in the current distribution model. In the case of the giraffe from a general perspective, differences between historical and current distribution indicate massive losses of suitable pixels, particularly in the Sahel and in the southern-Sahel region. Still in the southern and central Africa, suitable pixels extended throughout South Africa and Angola.

4.6 Predictions to 2080

Projections of distribution models for the future showed divergent results according to the dataset used (Fig. 7). Even though, the elephant is predicted to gain suitable cells regardless the prediction. This increment in suitable pixels is more evident when using the current distribution and it is expected this enlargement across the range, especially in the East and Central African regions. The giraffe's suitable habitat evolves differently according to the dataset that they are based on. Thus, projections from historical dataset exhibit an augment in suitable cells from West to East including Central and Southern African regions. In the opposite direction, projections made based on the current model distribution show a decrease in suitable areas, especially in Southern regions.

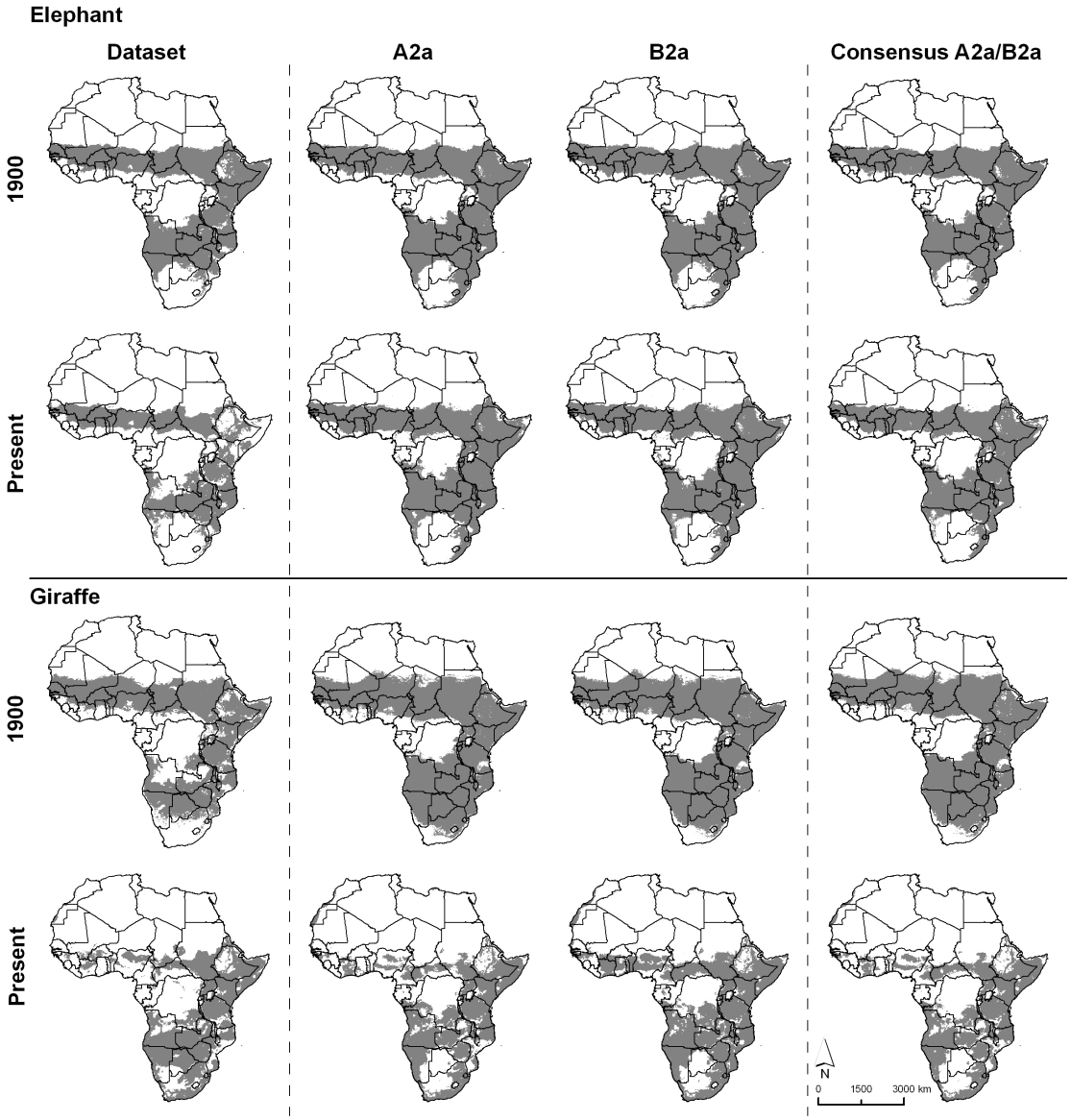

Fig. 7: Maps of presence-absence (consensus of all modeling approaches) for the elephant and giraffe in the beginning of the 20th century and present. Projections are represented by emission scenario and with a consensus map from an ensemble of both.

Comparing to 1900, elephants lost around 27% of its suitable habitat, and the giraffe around 20% (Fig. 8). Predictions made from the 1900 dataset revealed an augment in suitable area in both species more evident in the case of the giraffe (about 30%). In an opposite way, the forecasting for 2080 from current distribution show a slight increase in the elephant's suitable habitat (1.6%) and an impressive reduction in the giraffe's (26%).

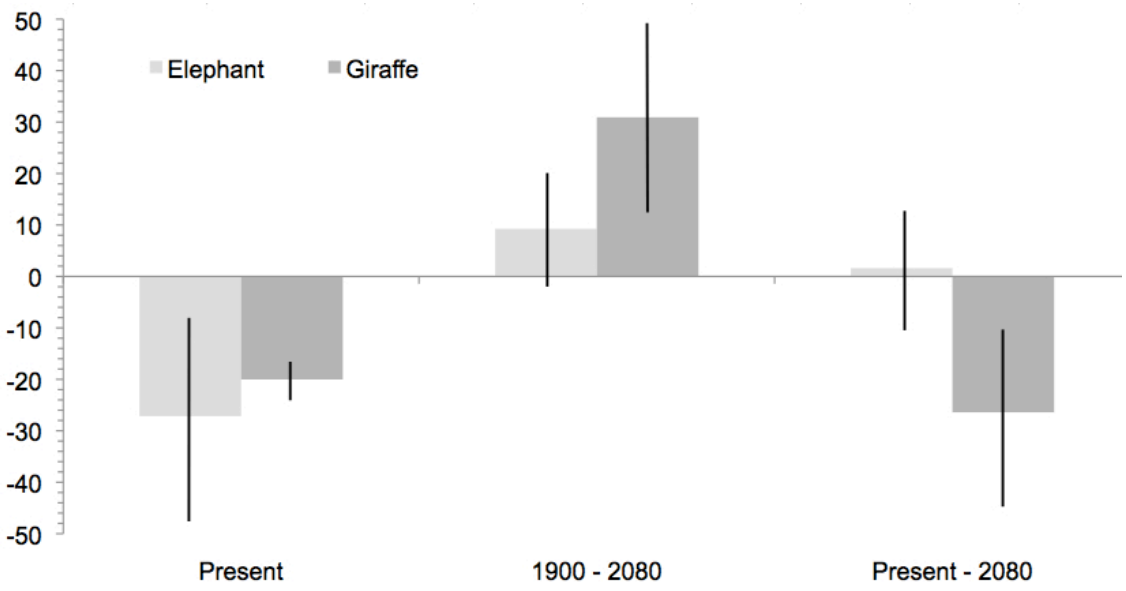

Fig. 8: Elephant and giraffe's evolution of suitable habitat. The beginning of the 20th century corresponds to 0.0. Black lines represent standard deviation of all four modeling techniques.

5. Discussion

This thesis aimed to compare the effects of modeling partial niches for future species' distributions due to climate change. To do so, we used two African species, the Savannah elephant and the Giraffe, three different timing scales and four different modeling approaches. In the following sections we will discuss the performance of ecological models, the effects of human activities on the range and ecological niche of the two species, and the effects of modeling partial niches and the consequences for future predictions under climate change scenarios.

1) Performance of ecological models

Whilst ecological modeling approach is generic, studies have reported variability across predictions from alternative models indicating that have a major influence on species distribution results (Araújo *et al.*, 2005; Pearson *et al.*, 2006). Uncertainties associated with different assumptions, algorithms and parameterizations raised methodological issues (Pearson *et al.,* 2006), particularly if addressing ecological questions. Regardless of great modeling performance, our predictions presented some inconsistencies across approaches, meeting what has been documented in the literature (Pearson *et al.,* 2006). Dissimilarities between predictions demonstrated to be more significant when using Present dataset than 1900 dataset (see Fig. S2). The number and spatial distribution of the presence points and the differences between algorithms and modeling procedures are the main causes of the dissimilarities found. The present data was smaller and spatially clustered whereas the 1900 dataset were able to cover a wider distribution. Models built from the present dataset were provided with less environmental information and the results came out biased and very different between modeling approaches. Further considering the differences between the four algorithms, their dataset requirements and modeling procedures (the use or not of replicates), two groups of predictions were easily identified. Thus, even though ENFA distribution models were the most dissimilar from all, they were easily paired with those from GLM. In the same way, models from Maxent and SIMAPSE demonstrated to be very consistent in their predictions. From the four modeling approaches selected, ENFA and GLM presented the lowest model performance with the lowest correct classification rate and spatial agreement (see Tab. 2 and Tab. S3.1). Although ENFA exhibits the advantage of not requiring absence data, it has been reported to be a less popular method to assess species distribution (Hirzel *et al.,* 2001). ENFA distribution models also showed to be the main reason for

the deviation between modeling approaches (see Figs. S3). On the other hand, GLM, a presence-absence method, due to all the limitations associated with absence data have been put aside in relation to other method. From all the uncertainties, limitations and inconsistencies found, ENFA and GLM modeling approaches were discarded from discussion hereafter.

2) Effects of human activities on the range and ecological niche

The spatial distributions of both elephant and giraffe have been changing since the beginning of the 20h century, mainly due to human activities. From an overview, the elephant's distribution contracted, especially in marginal areas, becoming extremely fragmented in some others (Fig 7). Dividing the African's continent by its main regions, we can identify three areas where the habitat suitability changed the most. Suitable pixels in West Africa, particularly from Senegal to Guinea almost disappear. In the East region, countries as Somalia, Ethiopia and Kenya that were classified as suitable for the elephant in the early 1900s, shifted to small and sparse suitable areas in the current distribution model (Barnes, 1999; Blanc *et al.*, 2007). The same pattern happened in Angola and Namibia that became regions with a high loss of suitable habitat. The case of the giraffe is ambiguous. In a general perspective, since the beginning of the 20th century, the species suitable habitat losses are massive, particularly in the Sahel and in the southern-Sahel region. Small and dispersed patches represent current distribution across these regions. Still, in southern and central Africa, suitable habitats extended throughout South Africa and Angola.

The changes on species spatial distribution result from the combination of human-induced pressures, e.g. poaching and habitat fragmentation that ultimately led to ecological niche shifts. Since the beginning of the 20th century the climatic space of both species diminished and their distributions converged from places with more extreme values where it became, apparently, intolerant (see Fig. 5). The loss of the climate space resulted from the contraction of the extremes (less than 400 mm and more than 1500 mm in annual precipitation) for both species, and the loss of a central portion (from 20.0 to 40.0 ◦ in temperature seasonality) in giraffe. Additionally, from 1900 to present, marginality and tolerance exhibited the same pattern for both species with the increase of the marginality and decrease of tolerance. The increase of marginality, particularly significant in giraffe, demonstrates that both species have been pushed away from their ecological optimum. Furthermore, the decrease of tolerance suggests that the ecological niches of both species have become more specialized.

Since the beginning of the 20th century, both elephant and giraffe have been targets of human persecution. Populations have been exterminated and their distribution contracted dramatically throughout Africa. Margin regions were the most affected, populations from West Africa and Sahara-Sahel regions were reduced to scattered patches. The decline of the edge populations reflected on species climatic space and changes in marginality and tolerance. The elephant and the giraffe lost environmental plasticity at the same time that they were pushed to sub-optimal habitats.

3) Effects of modeling partial niches and the consequences for future predictions under climate change

Modeling species distributions takes the assumption that the full niche has been captured and characterised. However, the availability of species data, the information biases or even the incomplete coverage of species distribution limited the access to the complete niche. Furthermore, with the recent human pressures, species populations have become extinct, which affects the species realized niche. Modeling these partial niches has major influence when futures predictions are made under climate change scenarios. Particularly the elephant is expected to gain suitable area apart from the dataset used (See Fig. 7; Fig. 8 and Tab. S4). However, the predictions of giraffe distributions differ according to the dataset. Predictions from the 1900 dataset indicate an expansion on distribution, on the other hand, predictions made based on the present distribution show a decrease in suitable areas. The lost of climatic space due to human pressure has a big impact on giraffes predictions.

5.1 Conclusions

This study represents an effort to identify the impact of human activities in large mammals in the last century and trough the future. Results from this work were expected to act like a warning tale when using blindly data for current species distributions. For example: predicting future ranges using partial-niches due to current range contraction and limited information regarding future climate changes, may result in biased predictions. The calculation of models based in partial niches may lead to severe underestimations and undermine the effectiveness of conservation measures to respond to climate change challenges. To overcome this problem, researchers should try to work with data that represents the full-niche of the target species.

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Supplementary material

Fig. S1: Spatial distributions of presence datasets for model species in both time periods.

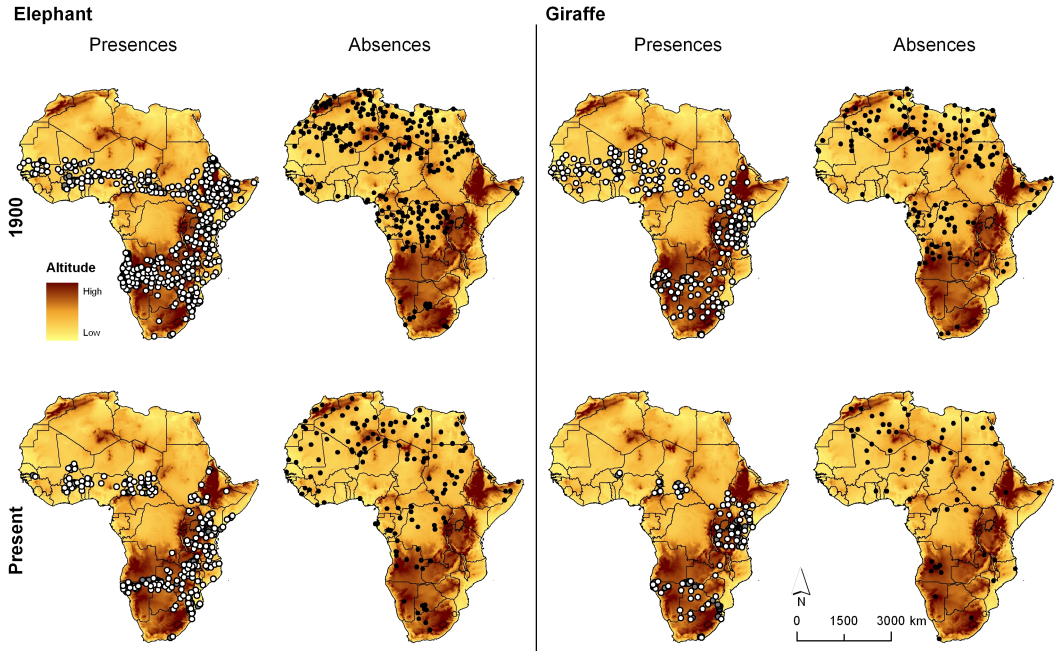
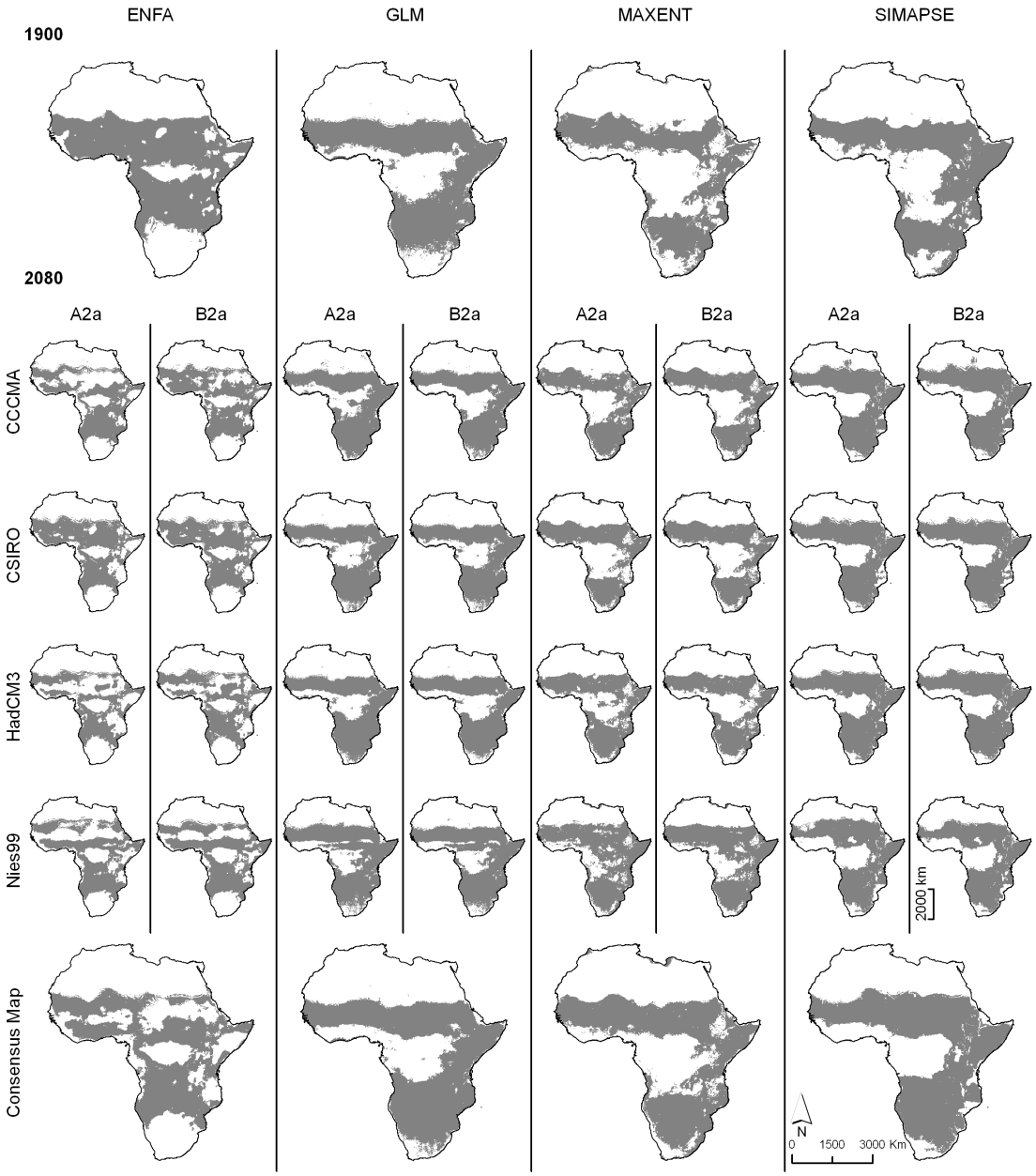


Fig. S2: Presence/absence distributions for each species according each dataset and corresponding predictions to 208

Giraffe


ENFA
GLM
MAXENT
SIMAPSE
1900
2080
A2a
B2a
CCCMA
CSIRO
HadCM3
Nies99
Consensus Map
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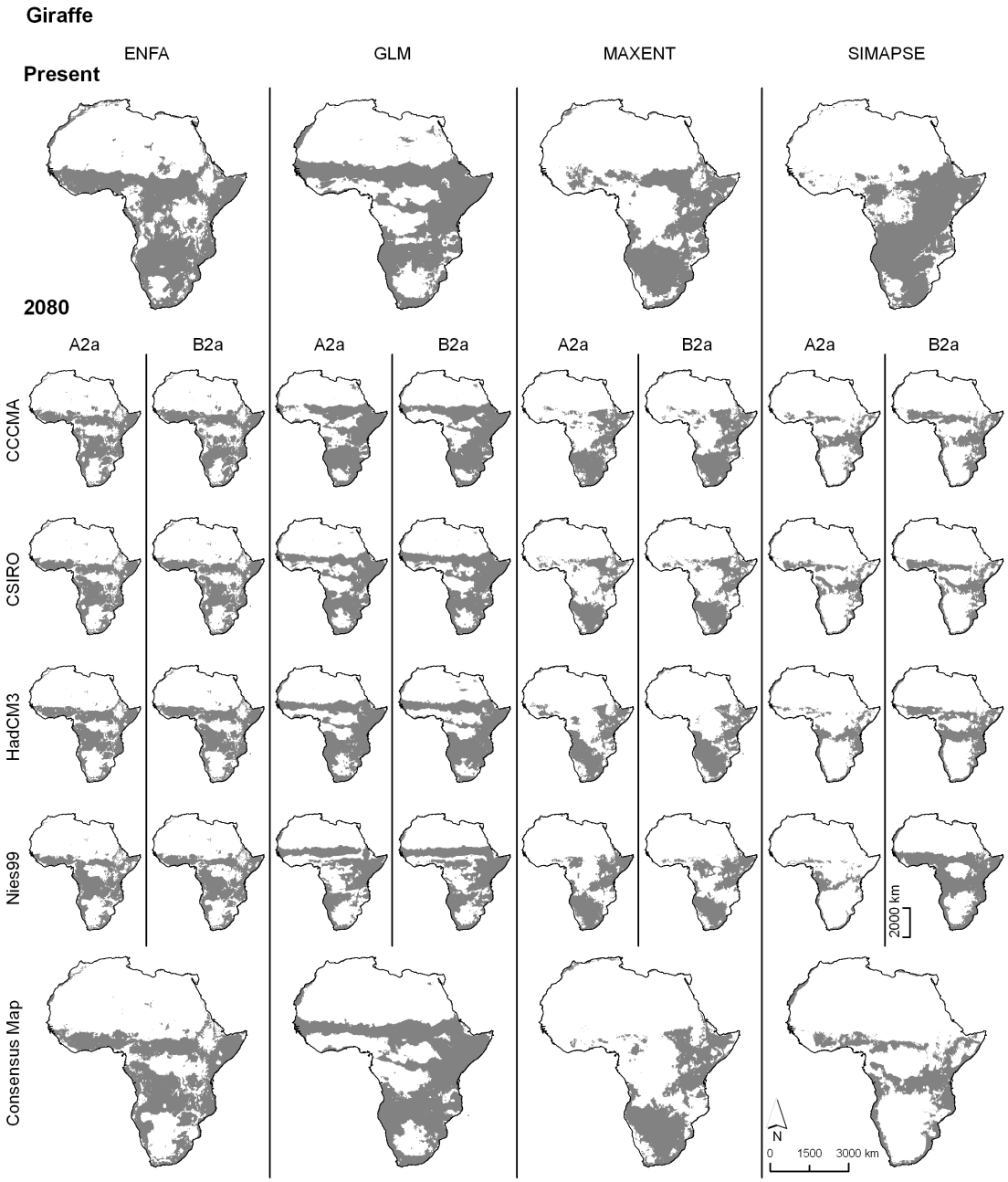
Giraffe
ENFA
GLM
MAXENT
SIMAPSE
Present
2080
A2a
B2a
CCCMA
CSIRO
HadCM3
Nies99
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2000 km
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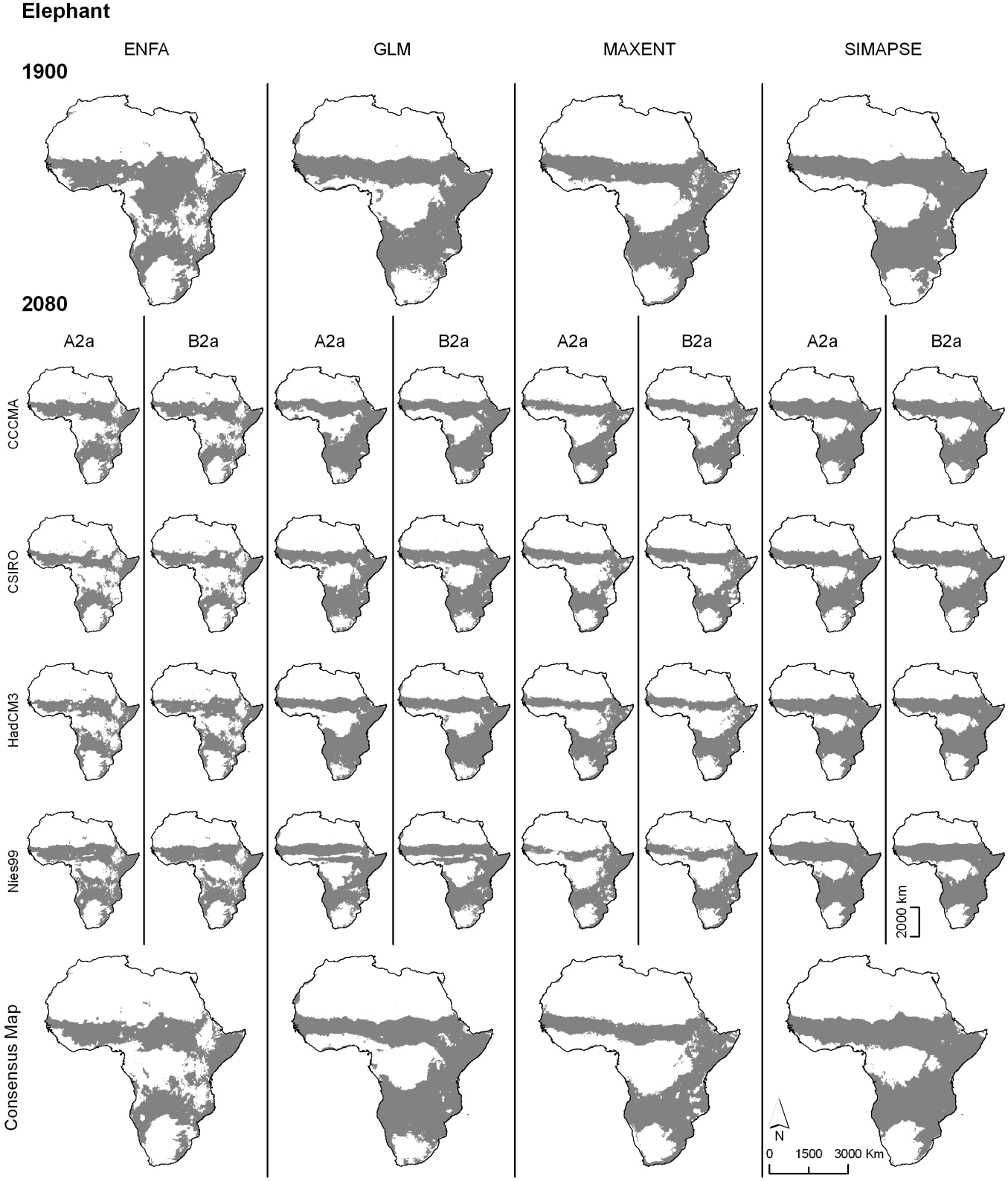
Elephant
ENFA
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2000 km
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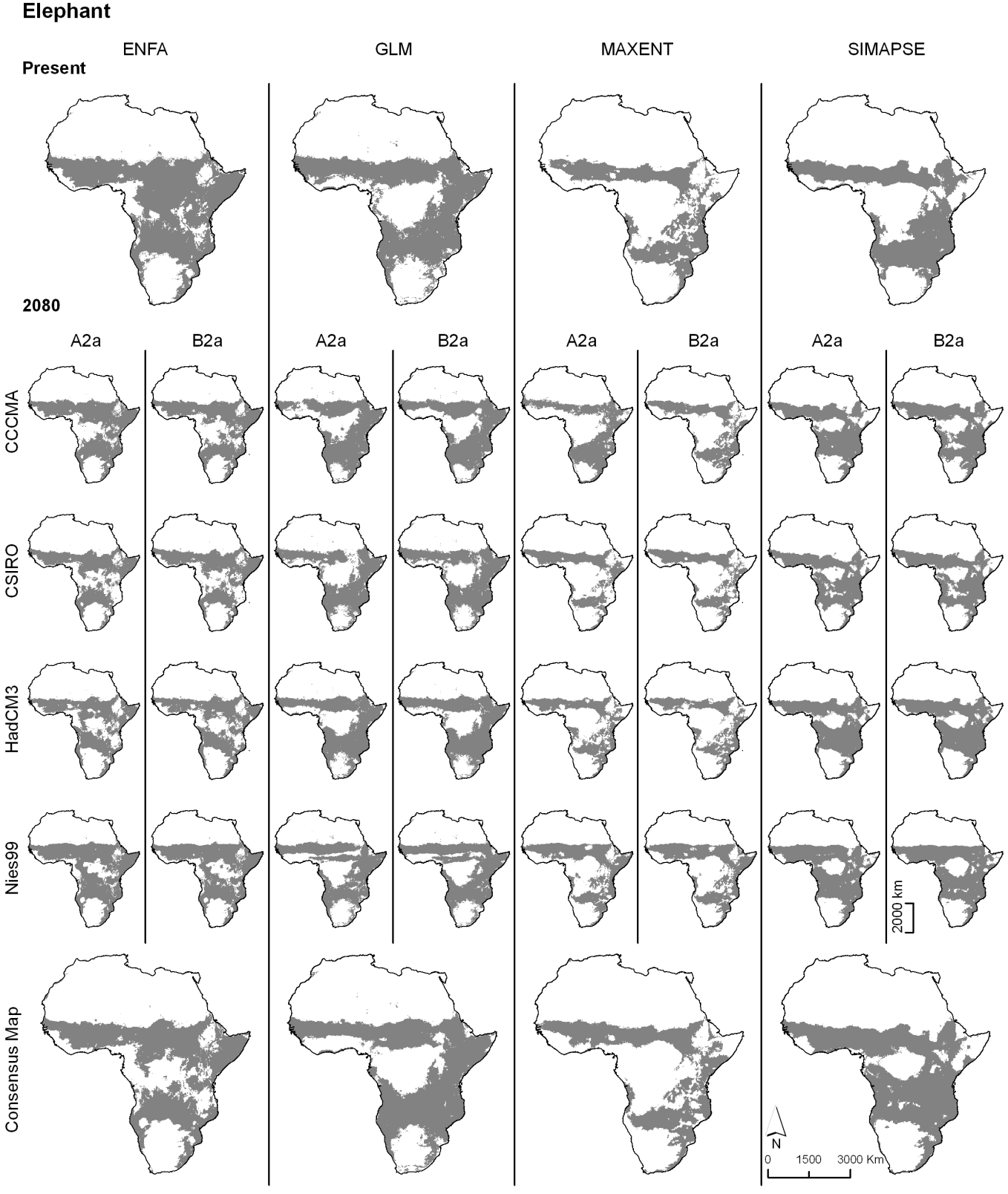
Elephant
ENFA
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Present
2080
A2a
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Consensus Map
2000 km
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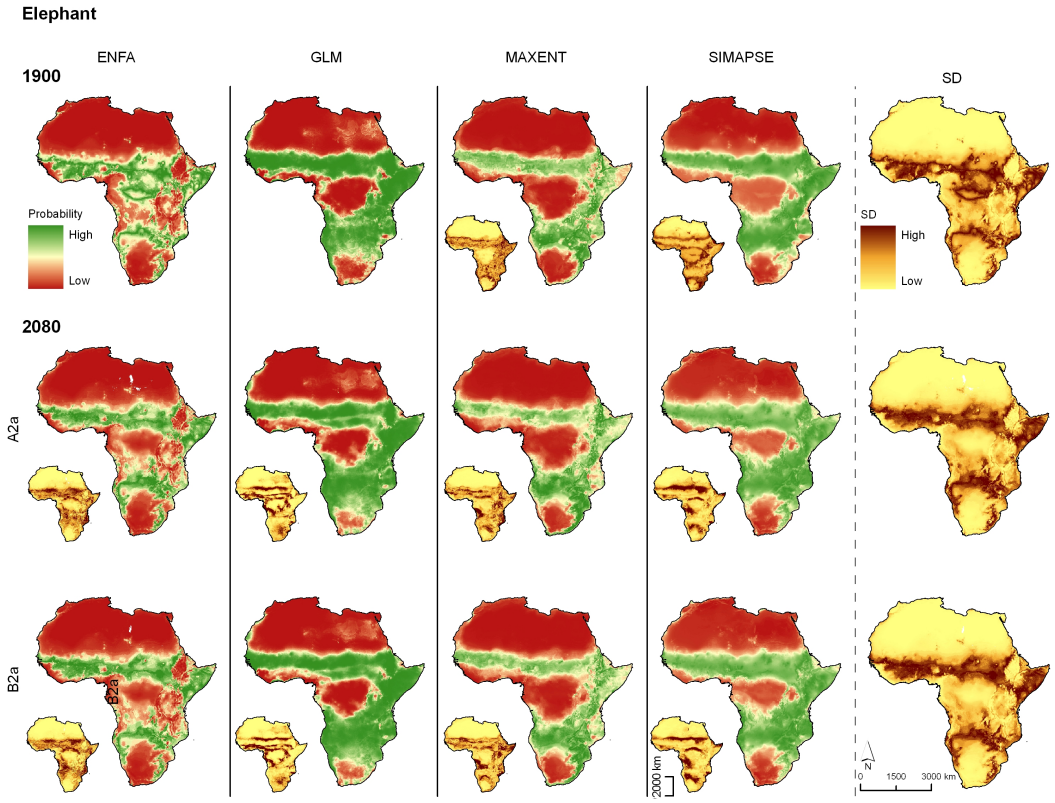
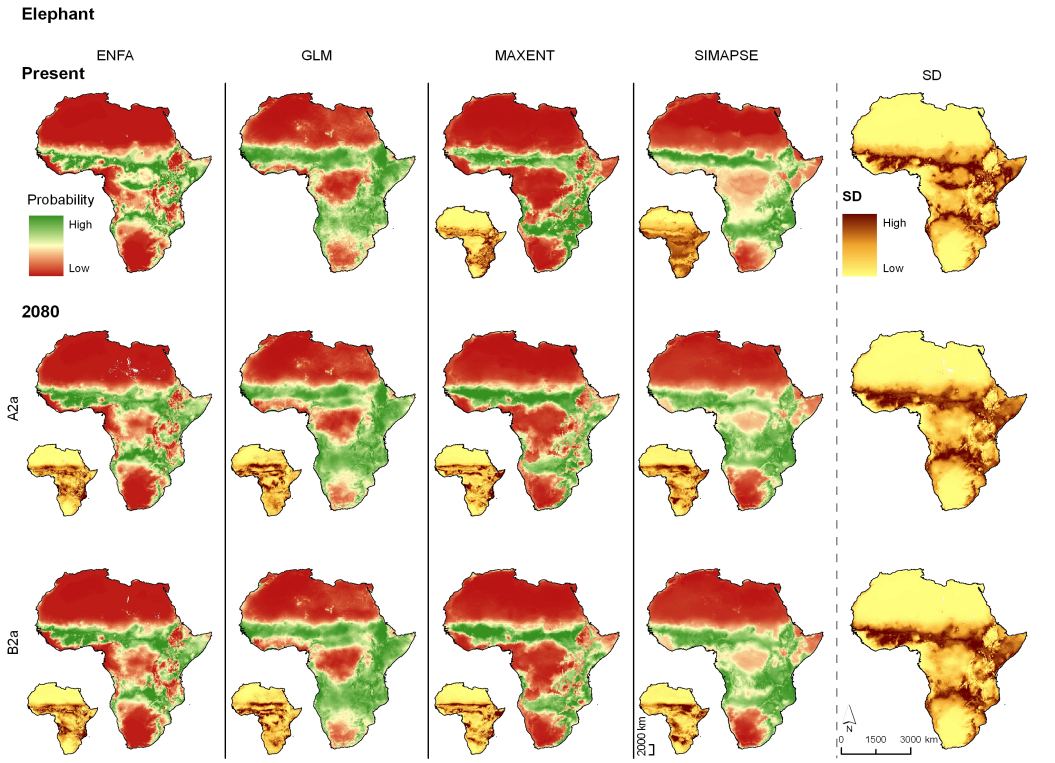
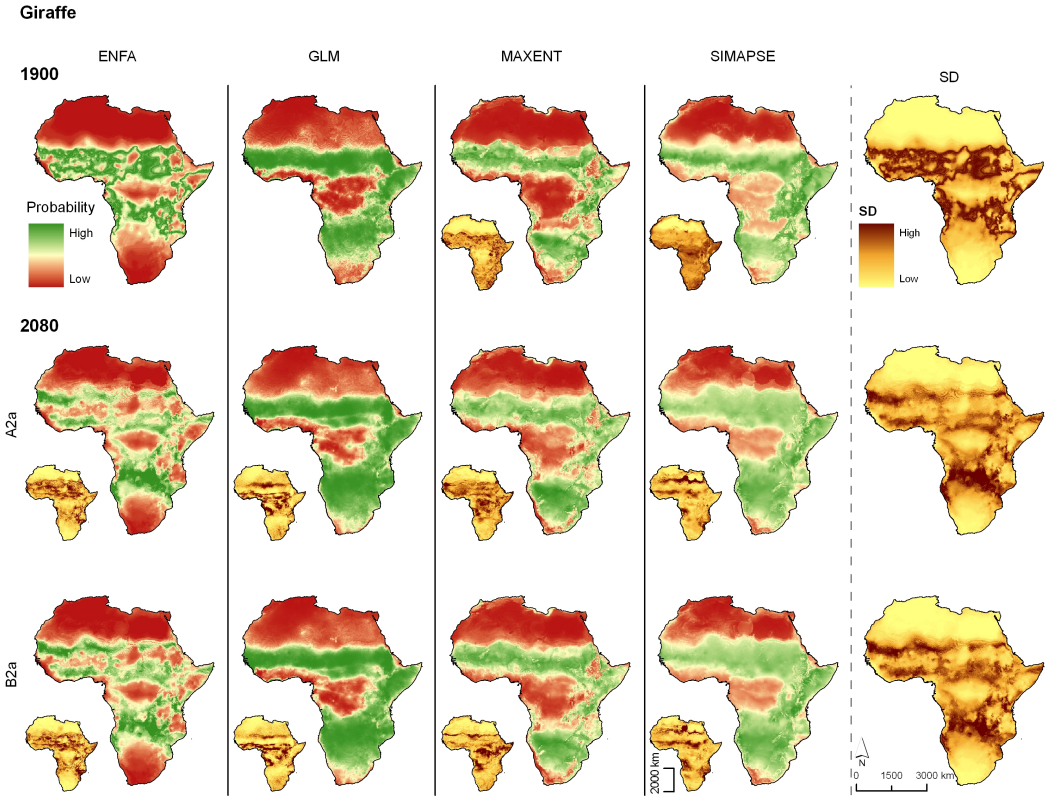
Fig. S3: Maps of probability of distribution for both species regarding each dataset and modeling technique. Standard deviation presented between replicates (Maxent and Simapse) and between modeling approaches.






Giraffe
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A2a
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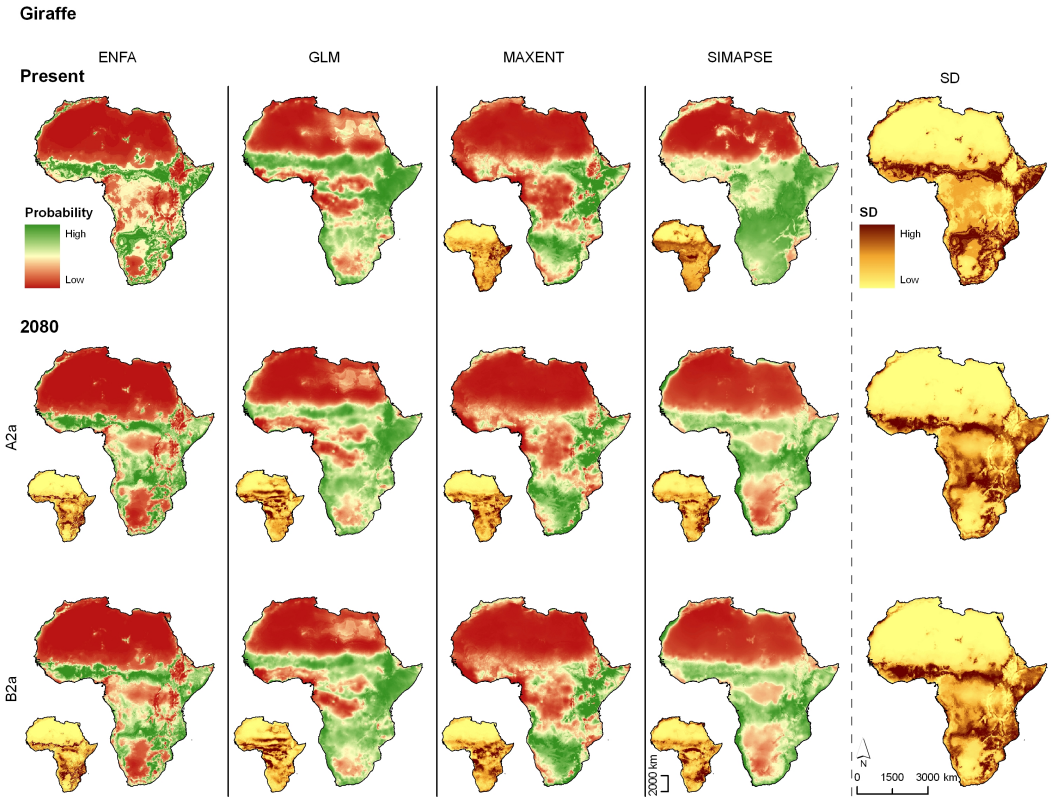
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Probability
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A2a
B2a
2000 km
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Supplementary material

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Table S2 – Range of values from the environmental factors used for model the distribution of selected species in the study area.

	Present/1900		A2a								B2a							
			CCCMA		CSIRO		HadCM3		Nies99		CCCMA		CSIRO		HadCM3		Nies99	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Altitude	-119	3884	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ruggedness	0	1894	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annual Mean Temperature (BIO 1)	5	30	5	36	5	35	6	36	7	36	3	33	4	35	4	34	5	35
Temperature Seasonality (BIO 4)	11	927	20	991	25	885	26	999	27	963	21	963	26	890	20	961	24	945
Max Temperature of Warmest Month (BIO 5)	12	48	11	54	10	53	11	55	13	56	10	52	10	52	10	53	11	54
Min Temperature of Coldest Month (BIO 6)	-8	22	-10	27	-7	26	-9	28	-6	27	-11	26	-8	26	-10	26	-7	26
Temperature Annual Range (BIO 7)	8	42	8	45	8	41	8	45	8	45	8	44	8	41	8	45	7	44
Annual Precipitation (BIO 12)	0	4208	0	4311	0	4261	0	5922	0	4598	0	4663	0	4272	0	1403	0	4335
Precipitation of Wettest Month (BIO 13)	0	1119	0	1336	0	1110	0	1335	0	1125	0	1589	0	1154	0	170	0	1080
Precipitation of Driest Month (BIO 14)	0	160	0	165	0	142	0	161	0	165	0	183	0	143	0	280	0	155
Precipitation Seasonality (BIO 15)	0	223	0	335	0	258	0	270	0	332	0	328	0	263	0	5852	0	273

Tables S3 - Measures of contibution of enviromental variables to the ecological models for the target species for all modeling approaches.

Table S3.1 – Importance of ecogeographical variables measured at the first axis derived from ecological-niche factor analysis (ENFA) for the elephant and giraffe. Values for 1900 and Present datasets.

Elephant

1900

	1	2	3	4	5	6	7	8	9	10	11
Altitude	0.267	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ruggedness	0.265	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Annual Mean Temperature	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Temperature Seasonality	-0.488	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Max Temperature of Warmest Month	-0.291	-0.463	0.463	0.463	0.463	0.463	-0.463	-0.463	-0.463	-0.463	0.463
Min Temperature of Coldest Month	0.205	0.525	-0.525	-0.525	-0.525	-0.525	0.525	0.525	0.525	0.525	-0.525
Temperature Annual Range	-0.339	0.714	-0.714	-0.714	-0.714	-0.714	0.714	0.714	0.714	0.714	-0.714
Annual Precipitation	0.190	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Wettest Month	0.412	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Driest Month	-0.157	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation Seasonality	0.385	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Present

	1	2	3	4	5	6	7	8	9	10	11
Altitude	0.115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ruggedness	0.211	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Annual Mean Temperature	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Temperature Seasonality	-0.477	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Max Temperature of Warmest Month	-0.295	0.463	0.463	0.463	-0.463	-0.463	-0.463	0.463	-0.463	0.463	-0.463
Min Temperature of Coldest Month	0.275	-0.525	-0.525	-0.525	0.525	0.525	0.525	-0.525	0.525	-0.525	0.525
Temperature Annual Range	-0.394	-0.714	-0.714	-0.714	0.714	0.714	0.714	-0.714	0.714	-0.714	0.714
Annual Precipitation	0.257	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Wettest Month	0.467	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Driest Month	-0.117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation Seasonality	0.312	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Giraffe

1900

	1	2	3	4	5	6	7	8	9	10	11
Altitude	0.161	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ruggedness	-0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Annual Mean Temperature	0.235	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Temperature Seasonality	-0.458	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Max Temperature of Warmest Month	-0.094	-0.463	0.463	0.463	0.463	-0.463	0.463	-0.463	-0.463	0.463	-0.463
Min Temperature of Coldest Month	0.258	0.525	-0.525	-0.525	-0.525	0.525	-0.525	0.525	0.525	-0.525	0.525
Temperature Annual Range	-0.251	0.714	-0.714	-0.714	-0.714	0.714	-0.714	0.714	0.714	-0.714	0.714
Annual Precipitation	0.039	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Wettest Month	0.297	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Driest Month	-0.202	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation Seasonality	0.664	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Present

	1	2	3	4	5	6	7	8	9	10	11
Altitude	0.381	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ruggedness	0.212	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Annual Mean Temperature	-0.179	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Temperature Seasonality	-0.510	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Max Temperature of Warmest Month	-0.482	-0.463	-0.463	0.463	-0.463	-0.463	0.463	0.463	-0.463	0.463	0.463
Min Temperature of Coldest Month	0.184	0.525	0.525	-0.525	0.525	0.525	-0.525	-0.525	0.525	-0.525	-0.525
Temperature Annual Range	-0.448	0.714	0.714	-0.714	0.714	0.714	-0.714	-0.714	0.714	-0.714	-0.714
Annual Precipitation	0.112	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Wettest Month	0.177	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation of Driest Month	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Precipitation Seasonality	0.082	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S3.2– Importance of ecogeographical variables measured by the significance level derived from Generalized Linear Models. Values of significance level are represented in the last column.

Elephant

1900

	Estimate	Std.	Error	z value	Significance
(Intercept)	8.384	2.116	3.963	0.000	***
Altitude	0.001	0.001	0.957	0.339	
Ruggedness	0.003	0.002	1.440	0.150	
Annual Mean Temperature	0.789	0.259	3.051	0.002	**
Temperature Seasonality	-0.023	0.003	-6.932	0.000	***
Max Temperature of Warmest Month	-0.140	0.345	-0.405	0.685	
Min Temperature of Coldest Month	-0.689	0.337	-2.049	0.040	*
Temperature Annual Range	-0.128	0.316	-0.405	0.686	
Annual Precipitation	-0.017	0.002	-8.708	0.000	***
Precipitation of Wettest Month	0.077	0.009	8.415	0.000	***
Precipitation of Driest Month	0.018	0.021	0.883	0.377	
Precipitation Seasonality	-0.044	0.008	-5.185	0.000	***

Present

	Estimate	Std.	Error	z value	Significance
(Intercept)	2.157	1.835	1.175	0.240	
Altitude	0.000	0.001	0.343	0.732	
Ruggedness	0.008	0.003	2.416	0.016	*
Annual Mean Temperature	0.441	0.257	1.720	0.085	.
Temperature Seasonality	-0.010	0.003	-3.326	0.001	***
Max Temperature of Warmest Month	-0.444	0.338	-1.313	0.189	
Min Temperature of Coldest Month	-0.015	0.336	-0.044	0.965	
Temperature Annual Range	0.286	0.319	0.895	0.371	
Annual Precipitation	-0.007	0.001	-4.680	0.000	***
Precipitation of Wettest Month	0.036	0.007	4.761	0.000	***
Precipitation of Driest Month	0.009	0.019	0.491	0.624	
Precipitation Seasonality	-0.015	0.008	-1.745	0.081	.

Signif. codes:

0	***
0,001	**
0,01	*
0,05	.
0,1	" "

Giraffe

1900

	Estimate	Std.	Error	z value	Significance
(Intercept)	-1.949	1.350	-1.444	0.149	
Altitude	0.001	0.001	1.547	0.122	
Ruggedness	0.001	0.002	0.397	0.691	
Annual Mean Temperature	0.636	0.238	2.665	0.008	**
Temperature Seasonality	-0.013	0.003	-4.203	0.000	***
Max Temperature of Warmest Month	0.242	0.343	0.707	0.480	
Min Temperature of Coldest Month	-0.838	0.331	-2.534	0.011	*
Temperature Annual Range	-0.335	0.318	-1.053	0.292	
Annual Precipitation	-0.010	0.002	-5.868	0.000	***
Precipitation of Wettest Month	0.048	0.008	5.712	0.000	***
Precipitation of Driest Month	0.056	0.016	3.463	0.001	***
Precipitation Seasonality	-0.009	0.006	-1.537	0.124	

Present

	Estimate	Std.	Error	z value	Significance
(Intercept)	8.439	3.827	2.205	0.027	*
Altitude	0.000	0.001	0.357	0.721	
Ruggedness	0.000	0.005	0.064	0.949	
Annual Mean Temperature	-0.013	0.387	-0.034	0.973	
Temperature Seasonality	-0.015	0.006	-2.490	0.013	*
Max. Temperature of Warmest Month	-0.133	0.532	-0.250	0.803	
Min. Temperature of Coldest Month	0.026	0.497	0.053	0.958	
Temperature Annual Range	0.203	0.483	0.420	0.674	
Annual Precipitation	-0.010	0.003	-3.537	0.000	***
Precipitation of Wettest Month	0.041	0.015	2.742	0.006	**
Precipitation of Driest Month	0.066	0.044	1.506	0.132	
Precipitation Seasonality	-0.032	0.013	-2.489	0.013	*

Table S3.3 - Importance of ecogeographical variables measured by percentage of contribution derived from Maximum entropy approach (Maxent). Values of training/test AUC and percentage of contribution of each EGV are represented for the elephant and giraffe for the *1900* and *Present* models.

% of Contribution of EGVs	Elephant		Giraffe	
	1900	Present	1900	Present
Altitude	3,6	6,5	4,8	7,9
Ruggedness	3,5	4,3	4,7	5,9
Annual Mean Temperature	2,9	4,4	4,1	4,6
Temperature Seasonality	42,6	15,7	11,1	10,4
Max. Temperature of Warmest Month	1,3	1,7	2,8	3,4
Min. Tempenerature of Coldest Month	2,3	2,1	3,4	1,2
Temperature Annual Range	3,8	4	5	2,6
Annual Precipitation	26,3	40,4	17,7	41,5
Precipitation of Wettest Month	5,5	12	32	14,9
Precipitation of Driest Month	1,6	1,4	1,9	2
Precipitation Seosonality	6,6	7,5	12,6	5,6
Training AUC	0,895	0,939	0,898	0,897
Test AUC	0,829	0,874	0,786	0,822

Table S3.4 – Importance of ecogeographical variables measured by square sum of partial derivates from Artificial Neural Network approach (Simapse). Values of AUC and values of contribution of each EGV are represented for the elephant and giraffe for the *1900* and *Present* models.

	Elephant				Giraffe			
	1900		Present		1900		Present	
Contribution of EGVs (square sum of partial derivates)	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
Altitude	21.7	49.2	12.5	30.4	6.1	8.6	9.6	20.2
Ruggedness	4.5	7.6	6.0	16.7	22.9	54.0	5.1	11.4
Annual Mean Temperature	16.3	44.9	16.4	27.3	22.1	48.6	3.4	10.8
Temperature Seasonality	44.5	60.4	36.5	79.3	43.2	70.3	9.6	14.9
Max Temperature of Warmest Month	9.5	14.6	18.1	24.3	10.6	24.1	3.0	5.9
Min Temperature of Coldest Month	8.3	21.6	11.9	20.0	11.3	20.8	1.2	2.3
Temperature Annual Range	7.3	12.0	3.3	5.4	4.4	7.2	1.7	3.6
Annual Precipitation	36.3	61.3	50.1	92.4	65.2	149.9	8.4	17.4
Precipitation of Wettest Month	17.8	17.3	43.9	55.3	18.6	28.5	4.3	7.2
Precipitation of Driest Month	16.4	26.2	19.1	29.2	15.5	39.0	2.9	6.7
Precipitation Seasonality	27.4	27.1	33.1	37.2	14.7	21.2	2.3	5.4
Chosen net	11.000	35.426	23.000	47.718	19.000	59.380	39.000	78.835
Training Error	32.261	2.576	12.919	2.161	22.920	2.729	6.311	1.910
AUC Roc	0.826	-	0.914	-	0.796	-	0.891	-
AUC Precision	0.778	-	0.879	-	0.788	-	0.888	-
Test Error	10.301	1.191	4.701	0.988	6.685	0.892	2.890	0.861

Table S4 - Spatial agreement between species distribution models.

Table S4.1 - Spatial agreement between modeling techniques according each species dataset.

	Giraffe	1900			
		ENFA	GLM	MAXENT	SIMAPSE
Present	ENFA	-	0.492 (0.745)	0.317 (0.656)	0.379 (0.688)
	GLM	0.387 (0.696)	-	0.612 (0.808)	0.700 (0.851)
	MAXENT	0.444 (0.730)	0.491 (0.755)	-	0.674 (0.841)
	SIMAPSE	0.411 (0.711)	0.455 (0.734)	0.539 (0.786)	-

	Elephant	1900			
		ENFA	GLM	MAXENT	SIMAPSE
Present	ENFA	-	0.497 (0.752)	0.505 (0.759)	0.507 (0.757)
	GLM	0.583 (0.794)	-	0.770 (0.888)	0.857 (0.930)
	MAXENT	0.419 (0.719)	0.472 (0.760)	-	0.792 (0.898)
	SIMAPSE	0.442 (0.727)	0.647 (0.834)	0.660 (0.859)	-

	Giraffe	Present - 2080			
		ENFA	GLM	MAXENT	SIMAI
1900 - 2080	ENFA	-	0.262 (0.631)	0.242 (0.624)	0.347 (
	GLM	0.316 (0.672)	-	0.713 (0.856)	0.762 (
	MAXENT	0.278 (0.690)	0.406 (0.724)	-	0.650 (
	SIMAPSE	0.447 (0.771)	0.211 (0.640)	0.247 (0.733)	-

	Elephant	Present - 2080			
		ENFA	GLM	MAXENT	SIMAPSE
1900 - 2080	ENFA	-	0.601 (0.806)	0.571 (0.801)	0.703 (0.854)
	GLM	0.594 (0.805)	-	0.764 (0.885)	0.801 (0.901)
	MAXENT	0.525 (0.787)	0.515 (0.778)	-	0.712 (0.858)
	SIMAPSE	0.552 (0.786)	0.575 (0.795)	0.460 (0.756)	-

Table S4.2 – Spatial agreement between emission scenarios regarding each species dataset and modeling tool.

	Elephant	Giraffe
	Present 2080	
ENFA	0.906 (0.956)	0.893 (0.952)
GLM	0.909 (0.956)	0.873 (0.939)
MAXENT	0.880 (0.955)	0.897 (0.962)
SIMAPSE	0.890 (0.948)	0.611 (0.877)
Consensus	0.894 (0.949)	0.773 (0.907)
	1900 2080	
ENFA	0.907 (0.958)	0.784 (0.896)
GLM	0.928 (0.965)	0.917 (0.958)
MAXENT	0.898 (0.953)	0.884 (0.942)
SIMAPSE	0.953 (0.976)	0.952 (0.976)
Consensus	0.944 (0.973)	0.926 (0.963)

Table S4.3 – Spatial agreement between time periods and projections for the elephant and giraffe.

Elephant	**1900**	**Present**	**1900 - 2080**	**Present - 2080**
1900	-	-	-	-
Present	0.695 (0.859)	-	-	-
1900 - 2080	0.883 (0.943)	-	-	0.858 (0.930)
Present - 2080	-	0.726 (0.873)	-	-

Giraffe	1900	Present	1900 - 2080	Present - 2080
1900	-	-	-	-
Present	0.470 (0.752)	-	-	-
1900 - 2080	0.717 (0.857)	-	-	0.343 (0.662)
Present - 2080	-	0.694 (0.868)	-	-

Table S5 - The evolution of the suitability of the habitat for elephant and giraffe in comparison to the beginning of the 20th century. Values presented in N absolute, change absolute (in relation to 1900), percentage of change.

N absolute				
	1900	1900 - 2080	Present	Present - 2080
Giraffe	36825	48209	29454	27103
Elephant	36316	39669	26457	36895

Change absolute				
	1900	Present	1900 - 2080	Present - 2080
Giraffe	0	-7371	11384	-9722
Elephant	0	-9859	3353	579

% Change				
	1900	Present	1900 - 2080	Present - 2080
Giraffe	0	-20.0	30.9	-26.4
Elephant	0	-27.1	9.2	1.6